

ONTOGENETIC DEVELOPMENT IN SWIMMING  
ABILITY OF TWO SPECIES OF COLD-WATER MARINE  
FISH LARVAE AND THE ROLE OF TEMPERATURE

LU GUAN







**Ontogenetic development in swimming ability of two species of  
cold-water marine fish larvae and the role of temperature**

By

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## Abstract

This study examines the effect of temperature on the development of active swimming ability in the larvae of two cold-water fish species, the pelagic spawner *Gadus morhua* (Atlantic cod) and the bottom spawner *Myoxocephalus scorpius* (shorthorn sculpin). The first chapter provides a brief overview of studies on swim speed in larval fishes and how they have been used in studies of dispersal. The second chapter examines the development of critical swimming speed in larvae of the two species reared at different temperatures. These swimming tunnel experiments show that temperature has a clear effect on critical swimming ability of sculpin larvae as they increase in size and age. By contrast, a temperature effect on development of swimming ability in cod larvae was only observed with thermal summation age. Sculpin larvae hatched at a bigger size and stronger swim speed than cod larvae, and also exhibited faster development rate of swimming speed relative to both size and age than cod. The third chapter examines the influence of temperature on development of sustained swimming ability in larvae of the same two species. For sculpin larvae, temperature only has a significant effect on development of sustained swimming ability as a function of absolute age, although sustained swimming speed increased with both age and size. For cod larvae, however, there was a significant temperature effect on development of sustained swimming ability only as a function of size. Cod larval sustained swim speeds lagged behind those of sculpin larvae as a function of age because of the smaller size of cod larvae at hatch. The fourth chapter

presents larval transport simulations for Placentia Bay, Newfoundland, in which larvae were initially assumed to be entirely passive and thereby transported exclusively by mean currents. These results were compared to simulations that combined larval active swimming speeds with the influence of mean currents. These simulations, which were conducted for spring and summer temperatures, were then compared to field patterns of larval concentrations from multiple biological surveys in Placentia Bay. The simulations indicated that larvae of bottom-spawning sculpin could take advantage of currents and their strong swimming ability to influence dispersal and improve retention within the embayment, particularly in warmer water temperatures. Larvae of pelagic-spawning cod were almost entirely passive, irrespective of water temperature. Field patterns of cod and sculpin larvae were generally consistent with the simulations, particularly in the context of the active retention simulation for sculpin. This thesis demonstrates that active swimming by larval fish has the potential to significantly influence transport and dispersal, but this potential differs for species and environmental conditions.



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## **Introduction and Overview**

The pelagic spawner Atlantic cod and the demersal (bottom) spawner shorthorn sculpin both produce larvae that develop in the pelagic zone, and larval dispersal patterns during this early pelagic phase have important implications for marine fishes with different life histories, including spatial and temporal variability recruitment and population dynamics (Fisher and Bellwood, 2003). Recruitment in this thesis refers to survival beyond the initial period of high mortality associated with early life history stages. In recent decades, many studies have suggested that larval fish can actively modifying their dispersal and potentially influence recruitment variation. Although it is clear that oceanographic transport influences the dispersal of marine fish larvae, the extent to which active larval behaviour contributes to dispersal is a subject of debate (Roberts, 1998; Bellwood *et al.*, 1998; Cowen *et al.*, 2000; Fisher and Bellwood, 2003). Larval fish distribution patterns are likely dictated by a combination of active locomotory behaviour, larval duration, and physical mechanisms such as currents, tides, and winds. From an ecological perspective, the role of environmental temperature also has a complex influence on larval dispersal, in that temperature can often vary substantially on a seasonal and annual basis when reproductive propagules develop and disperse. The complex interaction of these variables suggests that controlled experimental studies are needed to address basic issues such as the swim speed and endurance of fish larvae and the extent to which active swimming behaviour and physical transport mechanisms contribute respectively to dispersal of

fish larvae.

The main purpose of this study is to examine the swimming performance of two species of cold-water marine fish larvae as they age and increase in size under different rearing temperatures. The specific questions addressed are: (1) how does swimming ability develop with increases in size and age during larval development, (2) how does swimming ability develop under different temperatures during larval development in each experimental species, (3) how does development of swimming ability of larvae compare between two particular pelagic and demersal spawners?

The study can be divided into four major components. The first chapter investigates the transport process and mechanisms during the early life phase of marine fish larvae, and then discusses the importance of active swimming behaviour of fish larvae in determining spatial and temporal patterns, population dynamics, and recruitment. Finally, it attempts to clarify the potential differences in swimming ability among different species (including demersal and pelagic spawners) and how they appear to be related to size, age, and environmental temperature. The second chapter examines the critical swimming speed of fish larvae over short distances and short time scales using the 'increased velocity' method. This chapter also compares the effect of temperature on critical swimming speed development in fish larvae of the two species with different life histories (pelagic and demersal spawners). The third chapter first

examines the sustained swimming speed of fish larvae, which is a measure of how long fish larvae can maintain a given swim speed, and then compares the effect of temperature on sustained swimming speed development in a pelagic and a demersal spawner. The fourth chapter places the findings on critical and sustained swimming speed in a field context. Using the swim speed data from Chapter 2, swim time data from Chapter 3, and current data from Placentia Bay, Newfoundland, I place them together in simulations of passive and active transport of fish larvae. Results of the simulations are then compared to field observations on fish larval concentrations in different seasons to determine whether passive or active models provide a better representation of natural patterns.

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## **Co-Authorship Statement**

All manuscripts of this thesis were co-authored with Paul Snelgrove; and Chapter 2 was also co-authored by Kurt Gamperl. In all instances, I was the principle contributor to project design and proposal, implementation of the lab research component, analysis of data and manuscript preparation.

Chapter 2 has been submitted to Journal of Experimental Marine Biology and Ecology.

# **Chapter 1 – Transport of fish larvae: The role of active swimming behavior and physical oceanography**

## **1.1 Introduction**

Many marine organisms exhibit complex life cycles that allow them to disperse to new habitats and avoid intraspecific competition and potentially reduce mortality related to depleted food resources or predation. In many fish species, dispersal to new habitat is achieved in part by a planktonic larval phase, but dispersal is complicated by the need to place propagules in a habitat suitable for survival and growth. Although many fish larvae have some swimming ability, relatively strong currents may transport them to unsuitable habitat. These complex processes raise the question of the extent to which fish larvae can contribute to early dispersal by active swimming, and how strength of ocean currents influences this process. Thus, what are the relative contributions of active swim behaviour and physical oceanographic mechanisms to transport and dispersal, and how does variation in environmental conditions affect these contributions? In order to answer these questions, there is a need for interdisciplinary studies that incorporate behaviour, larval duration, and physical oceanography to explain observed patterns and to generate predictive models of dispersal, recruitment, and population biology.

### *Historical Perspective*

In the past two decades, a primary focus in fish ecology has been to determine factors

that influence dispersal patterns, population size, and structure (Doherty and Williams, 1988). By the early 1980s there was a large body of literature suggesting that random recruitment events were the major determinants of population sizes. This perspective led to many studies on dispersal and recruitment patterns and by the late 1980's the consensus was that these patterns were driven by transport mechanisms and availability of new recruits, which depend heavily on processes that influence the pelagic larval stage (Stobutzki and Bellwood, 1997; Leis, 2006). The factors that influence larval fishes and their recruitment patterns have been a major focus of fish ecology for many years (Miller *et al.*, 1988; Leis, 1991a), and the numbers of larval studies has increased rapidly in recent decades. Part of this focus has been on understanding mechanisms underlying recruitment, and the need to understand the role of early life history stages as sources of variation in adult population size of exploited species.

The majority of marine fishes produce larvae that develop in the pelagic environment prior to arriving at a juvenile habitat, and eventually replenishing adult populations (Green and Fisher, 2004). The process of dispersing to and later arriving at suitable juvenile habitat is essential for the completion of the life cycle and plays an important role in population dynamics (Leis, 1991a; Caley *et al.*, 1996; Dudley *et al.*, 2000). Thus, a key question is the extent to which larvae can modify their patterns of dispersal and distribution through active swimming behaviour in order to locate

suitable juvenile habitat (Leis *et al.*, 1996; Leis and McCormick, 2002). Are larvae passive particles whose arrival at suitable settlement habitat is determined by local currents, or do they have some control over their own fate?

Multiple studies suggest that pattern in larval distribution has significant consequences for recruitment and population stability (Hare and Cowen, 1996). Prior to the late 1990's, the ability of larval fishes to influence their dispersal remained an area of considerable debate (Bellwood *et al.*, 1998; Roberts, 1998; Sale and Cowen, 1998). Although many authors argued that larval behaviour may be important in dispersal (reviewed by Leis, 1991a), few have applied behavioural components to specific theories and models. Several authors have attempted to explain distribution patterns without considering active swimming by larvae (Booth and Baretta, 1994; Roberts, 1997; Leis, 2006), including studies that model fish larvae as passive particles in simulations of dispersal and recruitment (e.g. Heath *et al.*, 1998). Nonetheless, in many instances, hydrological patterns alone cannot explain or predict observed distributions (Stobutzki and Bellwood, 1997). The dearth of behavioural studies in realistic flows, the applicability of laboratory experiments to field situations, and the inability of passive models to explain independently dispersal patterns in many instances suggest a need for interdisciplinary approaches that incorporate active swimming behaviour, pelagic larval duration, and physical oceanography. Recent studies have provided strong evidence that active swimming behaviour of larval fish

during the pelagic period can significantly contribute to their open water distribution patterns (Fisher *et al.*, 2000; Leis, 2006). For example, studies in tropical waters have shown that the transport of late-stage larval reef fish is far from passive, and that larvae are strong swimmers (Leis *et al.*, 1996; Leis, 2006), exhibiting high speeds (Leis and Carson-Ewart, 1997; Bellwood and Fisher, 2001; Leis, 2006), as well as excellent sustained swimming capabilities (Fisher *et al.*, 2000; Leis, 2006). These studies suggest that larvae are 'effective' swimmers with considerable control over their position and their swimming trajectory. Attributes of larval fish behaviour such as swimming ability are now being used with increasing frequency to improve mathematical models of dispersal-recruitment relationships (Armsworth, 2000; Cowen *et al.*, 2006).

## **1.2 The active process: swimming ability of fish larvae**

### *The influence of swimming ability on dispersal*

Dispersal patterns during the pelagic larval phase have important implications for many marine organisms, affecting the degree of genetic connectivity (Doherty *et al.*, 1995), levels of self-recruitment (Cowen *et al.*, 2000), and population dynamics. There has been considerable debate about the relative importance of active behaviour in determining dispersal and distribution patterns of fish larvae. The traditional view, which is still maintained by some authors, is that fish larvae have little behavioural influence on dispersal (e.g. Roberts, 1997). Other workers, however, have suggested



that larval behaviour, including vertical and horizontal movement, may influence dispersal patterns (e.g. Cowen *et al.*, 1993; Leis *et al.*, 1996; Stobutzki & Bellwood, 1997; Sponugle *et al.*, 2002), and passive drift cannot explain distributions (Leis, 1991a) or settlement patterns. There is mounting evidence that active larval movement helps to shape dispersal patterns and determine settlement success (Armsworth, 2000; Cowen *et al.*, 2000; Sponaugle *et al.*, 2002). Active swimming behavior can significantly increase the probability of successful arrival at a suitable juvenile habitat, may substantially alter dispersal patterns, and could increase self-recruitment in some marine populations (Fisher and Wilson, 2004). Oceanographers and modellers are now attempting to incorporate larval fish behaviour such as navigational and swimming abilities into models when examining or predicting how oceanographic processes may affect their distribution (Armsworth, 2000). For example, larval reef fishes develop strong swimming abilities at an early enough age to influence substantially their dispersal patterns (Fisher *et al.*, 2000; Leis, 2006). Genetic evidence suggests that these fishes use their swimming capabilities to limit rather than enhance dispersal (Doherty *et al.*, 1995). There is also considerable evidence from hydrodynamic studies suggesting that local retention and early development of swimming ability in some demersal-spawning reef fishes may have significant potential for population self-seeding (Fisher *et al.*, 2000).

#### *Other application of swimming ability*

Locomotory performance, including swimming speed and endurance, is related to other measures of ecological performance and fitness such as feeding rates (Hunter, 1981; Elsworth *et al.*, 2003), ability to escape from predators, and energy expenditure (Miller *et al.*, 1988). Larval swimming ability determines prey encounter rates by altering swimming speed in response to prey concentrations, and also influences mortality loss from predation (Miller *et al.*, 1988). Swimming speeds are also important for feeding models because speeds determine how large an area larvae can search for food (Hunter, 1981; Elsworth *et al.*, 2003).

### **1.3 Swimming modes and study methodology in fish larvae dispersal**

Three dominant swimming modes of fish have been considered by researchers: (1) sustained swimming speed, (2) critical swimming speed (Plaut, 2001), and (3) burst swimming speed (Beamish, 1978; Hammer, 1995). Critical swim speed represents an intermediate range (from 30 s to 200 min) between burst (maximum possible) and sustained (maintained for long periods of time) swim speed. This intermediate measure of swim speed provides an indication of maximum performance for short-term swimming. Although sustained swimming at a relatively constant speed is thought to be the most widespread behaviour and one used primarily in searching for food (Hunter, 1972), larvae may also swim in fast bursts during attack and escape responses.

### *Critical swimming speed*

Critical swimming speed ( $U_{crit}$ ) provides a measure of maximum swimming speed that fishes can maintain, but it also provides a mechanism to compare directly the development of swimming ability among species (Fisher and Bellwood, 2003; Leis, 2006), and a framework to measure effects such as temperature or oxygen levels on swimming. This method involves 'forced' swimming of larval fish at equivalent intervals of increasing speed until the fish can no longer maintain position in the swimming tunnel (Fisher and Bellwood, 2003). In this process, the length of time that fish are able to maintain position in the tunnel is less likely to be influenced by the observers than by the flow speed and time increments used.

The  $U_{crit}$  method has been used in the past primarily to examine the swimming speeds of larval tropical reef fishes and some temperate fishes (Stobutzki and Bellwood, 1994; Fisher *et al.*, 2000; Green and Fisher, 2004; Clark *et al.*, 2005; Leis, 2006). The biological implications of critical swimming speeds relate to the ability of larvae to cover short distances (<500 m) at high speeds and over short time scales (<30 min) (Fisher *et al.*, 2000). This type of swimming behaviour may be particularly important for larval movement over small scales such as between waves, slicks, and fronts, to migrate vertically between different current regimes that could modify broad-scale dispersal patterns, to move away from nursery areas at hatching, or to move between habitats (Fisher *et al.*, 2000; Job & Bellwood, 2000). It is not, however, directly

applicable to dispersal models.

#### *Sustained swimming ability*

Sustained swimming, which is fuelled by aerobic metabolism, is important during dispersal and long migrations that may cover distances up to thousands of kilometers (Elsworth *et al.*, 2003; Plaut, 2001). Flume-based sustained swimming experiments are carried out by swimming larvae at a single speed without food and rest until exhaustion (Stobutzki and Bellwood, 1997; Dudley *et al.*, 2000). This measure of swimming ability provides data on endurance swimming which represents a performance measure of maintained swimming ability as well as a measure of how pelagic larvae could modify their dispersal over extended periods of time (Stobutzki and Bellwood, 1997). There is an increasing need to obtain reliable estimates of sustained swimming abilities of larvae, and data obtained from sustained swimming studies have been recently incorporated into models that examine the effect of behavior on larval dispersal (Armsworth, 2000).

#### *Comparison of swimming speed among different species*

Until recently, most studies on larval fish swimming ability have focussed on tropical reef fish, but there have been several studies on temperate fish larvae. In 1-h tests, yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) swimming velocities ranged from less than 1 bl·s<sup>-1</sup> (body length per second) for newly hatched

larvae to  $3\text{--}4\text{ bl}\cdot\text{s}^{-1}$  for larvae longer than 9.5 mm (Houde, 1969). Sustained swimming speed of striped bass, *Morone saxatilis* in 10-h tests during early feeding (6–9 mm body length) increased from 1.7 to  $3\text{ bl}\cdot\text{s}^{-1}$  as the larvae grew (Meng, 1993). Later, Stobutzki and Bellwood (1994) showed that the short-duration swimming speeds of settlement-stage larval reef fishes are relatively high. *Pomacentrus amboinensis*, for example, averaged  $43.7\text{ cm}\cdot\text{s}^{-1}$ , or approx.  $40\text{ bl}\cdot\text{s}^{-1}$ . Leis et al. (1996) estimated that some coral-reef fish larvae swim as fast as  $30\text{ cm}\cdot\text{s}^{-1}$  in the field. Leis et al. (1996) and Leis & Carson-Ewart (1997) also recorded high swimming speeds  $> 60\text{ cm}\cdot\text{s}^{-1}$  for reef fish larvae in the field which were maintained for several minutes. Several other recent laboratory and field studies have confirmed that late-stage reef-fish larvae are strong swimmers (Stobutzki and Bellwood, 1994; 1997; 1998; Leis et al, 1996; Leis, 2006). The difference in swimming ability of tropical and temperate fish may be a result of developmental differences at different temperatures or differences among taxonomic orders being compared, which may confounding the comparisons. Most larvae of coral-reef fishes have fully developed fins at a smaller size than temperate species, even though they retain adaptations for pelagic life that lead result in them being regarded as larvae (Leis and Carson-Ewart, 1997). Most of these recent studies indicate that tropical and temperate fish larvae are capable swimmers with the capacity for substantial behavioural contributions to transport, but there is little data on swimming abilities of cold-water species.

*Experimental methodologies in studies of larval fish larvae swimming ability*

Information on the swimming abilities of fish is derived from either field or laboratory studies. Investigations on the abilities of early stage larval fish have been limited by difficulties in collecting and maintaining live, healthy individuals from the field. Direct tracking of larvae in the field (e.g. Leis and Carson-Ewart, 1997; 1998; Leis, 2006) can provide realistic data when larvae are swimming in the real ocean environment but this approach is limited because larval concentrations are so dilute in the pelagic environment and also difficult for tracking the same larvae through their ontogenic development. However, laboratory rearing provides a means of evaluating the biological capabilities of larval fishes throughout their development. By hatching and rearing larvae under controlled conditions, it is possible to obtain live specimens of known age and parentage in good condition at all developmental stages. It is also possible to do comparable experiments under controlled condition, however there is a need to clarify how laboratory experiments can be applied to the real ocean environment, with its complex influences on the larvae. Methods for lab measurement of swimming speeds of larval fish fall into two categories. First, larval swimming is recorded on film or videotape to document swim speed and behaviour, but this approach tends to restrict fish to smaller containers that are suitable for photographic purposes (Meng, 1993). The second approach is to use a swim tunnel or flume to test swimming ability against a current. This approach has generated substantial information on critical swimming speed and duration of sustained swimming

(Stobutzki and Leis, 1999). Swim tunnels are well suited for measurements over long periods, for comparisons of stamina at a range of flow speeds, or for rapid measures of relative abilities. It is especially useful for obtaining rapid, comparative measures in order to determine the effect of factors such as temperature or diet on swimming (Fisher and Bellwood, 2001).

#### **1.4 Factors that influence larval fish swimming behaviour**

##### *The role of temperature*

Individuals often experience a broad range of environmental temperatures, which is strongly associated with geographical variation. Temperature variation influences metabolism and related physiological processes, and also affects growth, development and performance. Thus, temperature effects encompass a broad range of physiological and behavioural capabilities (Green and Fisher, 2004) that are particularly important during early development, including the pelagic larval phase. Temperature effects have been studied more extensively than other abiotic influence.

Performance is an expression of the physiological and behavioural capabilities of organisms and in cold-blooded animals is influenced by change in temperature (Fuiman and Batty, 1997). Temperature causes direct variation in development of swim speed. Moreover, because temperature influences development rate, it can determine the timing and size of the organism at which ontogenetic transformation

occurs. Temperature-induced morphological changes also have indirect effects on the development of swimming performance, by accelerating or delaying the development of functional structures such as muscle, gills, and biochemical pathways (Taylor *et al.*, 1997).

For small aquatic organisms, motility depends both on internal, physiological processes and on external, physical properties of the fluid environment. The effect of temperature on physiological performance are well known (Huey, 1982), and underlying physiological mechanisms such as metabolic rate and muscle activity are likely to determine animal locomotion (Elsworth *et al.*, 2003). When swimming in cold water, larvae have to use their muscle fibres over an increasingly inefficient range of reduced velocities, which influences muscle efficiency and also limits swimming performance at different temperatures (Hunt von Herbing, 2002; Leis, 2006).

Viscosity is widely recognized as a critical hydrodynamic character at small scales. Because of the small size and slow movement of small fish larvae, the physical properties of water can have a profound influence on their motion above and beyond water characteristics such as turbulence and chemical properties. Generally, fish larvae inhabit intermediate or transitional flow Reynold's number ( $Re$ ) regimes that often range between 20 and 500, in which both viscous and inertial forces operate. Temperature may affect the hydrodynamic flow conditions of larvae swimming



through the physical effect on water viscosity (Hunt von Herbing, 2002; Leis, 2006).

Although these biophysical effects are minor compared to physiological and developmental changes, they may cause substantial influence in swimming behaviour.

The temperature effect on viscosity is greater in cold water than in warm water.

#### *The role of size in swimming ability*

Body size has long been recognized as a variable that has important effects on many aspects of the physiology, ecology, and behaviour of living organisms (Miller *et al.*, 1988). It is also one of the central factors in survival (Houde, 1989) and can result in profound differences in larval success (Miller *et al.*, 1988) through its influence on swimming ability and susceptibility to predation. Fish swimming relies on muscles to generate inertial forces in the surrounding water. The speed produced in fish is dependent on the length of the fish, as well as the frequency and amplitude of the tail beat and the effect of streamlining. Both within and among species, swimming abilities of fish larvae are positive functions of larval length.

#### **1.5 Passive processes: Physical oceanographic effects on larval fish transport**

Physical mechanisms can affect multiple biological factors such as reproductive location, larval transport, and movement to settlement habitat. Attempts to explain the observed spatial and temporal distributions of larvae have often required interplay between the active behaviour of larvae and passive physical processes from the

environment. The mechanisms that disperse and concentrate fish larvae include both large and small-scale influences on distribution patterns. In complex ocean environments, large-scale and regional currents, eddies, Taylor columns, wind forcing, tidal currents, oceanographic gyres, frontal zones, and hydrothermal plumes all can contribute to larval transport and dispersal. Currents produced by wind, tides, and thermohaline forces are particularly important in how they interact to move water on multiple spatial and temporal scales and in doing so they can concentrate and disperse reproductive propagules. Eddies are rotary currents that can form convergences, which can concentrate buoyant planktonic larvae. Wind patterns are perhaps the most temporally variable of the processes that influence larval distribution, and they can have dramatic effects on larval fish survival and settlement. Many studies show that wind-driven Ekman flow can transport the eggs and larvae from nearshore and offshore spawners towards or away from appropriate nursery grounds. Another major transport mechanism is tidal currents, which are a mechanism for onshore and offshore transport. These processes transport reproductive propagules are critical for maintaining habitat association or colonization of new habitat. The relatively poor swimming capability of early-stage fish larvae suggests that rate and direction of larval advection depends more on physical transport (Bradbury, 2001).

#### **1.6 Larval fish dispersal: a combination of biological and physical processes**

Most marine teleost fish species spawn a large number of small offspring that are

transported away from spawning areas. It is clear that dispersal is a complex combination of physical oceanographic and larval biological processes (Sponaugle and Cowen, 1997), but the extent to which larval behavior or ocean currents influence contributes has generated considerable debate for a long time (Roberts, 1997; 1998; Cowen *et al.*, 2000). The transport and return of larvae to a suitable juvenile habitat is critical to the population dynamics of marine organisms with complex life histories and has important implications for population connectivity (see Sponaugle *et al.*, 2002; Warner and Cowen, 2002). Identification of the biological and physical mechanisms involved with pelagic fish larval transport and prediction of larval trajectories with real-time flow conditions (Paris and Cowen, 2004) are becoming topics of considerable interest in ecology, oceanography, conservation, and management (Sponaugle *et al.*, 2005). Simple models can demonstrate the sensitivity of a given process to particular conditions, and more sophisticated models should help predict where, when, and how many larvae are likely to recruit to a given shoreline (Cowen, 2002).

### **1.7 Summary and study objectives**

Over the past decades, most studies on swimming ability have been restricted to tropical reef fishes and temperate fishes. Tropical and temperate reef fish larvae have been shown to be strong swimmers and their movement in the water column results from the interactive effects of hydrodynamics and larval swimming. Larvae have

swimming speeds that allow directional motion and control over their vertical position in the water column (Leis, 1991a). However, the generality of these results is unknown; results from tropical and temperate regions can neither be readily applied to cold-water species nor applied to larvae from different taxonomic orders.

The dynamic, pelagic environment encountered by marine fish larvae necessitates that researchers be well versed in the physical and biological oceanography of their study system. Aspects of behaviour that might affect transport and dispersal, such as depth selection and swimming direction, are poorly understood for most species (Leis *et al.*, 1996; Leis, 2006), and the data necessary to provide modellers with appropriate, adequate input on larval behaviour are generally lacking. To improve our understanding of dispersal processes and patterns during the early larval phase, there is an urgent need for interdisciplinary studies that include more comprehensive and realistic data on early life histories (Leis, 1991a; Cowen and Sponaugle, 1997).

The study of larval fish transport is driven by the need to understand distribution and population patterns in marine fish. Though there is a considerable body of literature on coral reef fish and, to a lesser extent temperate fish, there are indications of key differences between these species and also with respect to cold-water fishes that relate to temperature and species differences. Complementary studies are needed for cold water species that address the potential for behaviour and swimming ability and

mechanisms of active and passive dispersal processes that are important in planktonic marine larvae. Such information is crucial to understanding recruitment patterns and population dynamics of marine cold-water fishes.

Chapters 2 and 3 of this thesis attempt to address this information gap for cold ocean species. Specifically, in Chapter 2 I examine the critical swimming speed of fish larvae, which is a measure of maximum swimming speed over short distance and time scales by using the 'increased velocity' method. In this chapter, I compare the effect of temperature on critical swimming speed development in fish larvae of two species with different life histories (pelagic and demersal spawners). In Chapter 3, I examine the sustained swimming ability of fish larvae, which is a measure of swimming endurance of fish larvae. I also compare the effect of temperature on development of sustained swimming speed in the same species of fish larvae presented in Chapter 2. then, I use the swim speed data from Chapter 2, swim time data from Chapter 3 and current speed data from Placentia Bay, Newfoundland to simulate the passive and active transport of larvae to explore where they might disperse. Results of the simulations are then compared to field data on fish larval concentrations in different seasons to determine whether passive or active models provide a better representation of natural patterns.

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## **Chapter 2 - Ontogenetic changes in critical swimming speed of larvae of two species of cold-water marine fishes and the role of temperature**

### **2.1 Introduction**

Two key questions in marine ecology are how far propagules of benthic and demersal species or pelagic species disperse and how they locate suitable settlement sites (Bradbury and Snelgrove, 2000). These issues are central to understanding spatial and temporal patterns in marine environments, and recruitment variability in fisheries research. As noted by Leis and McCormick (2002), replenishment of adult population in many marine fishes occurs through a pelagic larval phase. Settlement of larvae or recently metamorphosed early juveniles to demersal habitats plays an important role in population dynamics and self-recruitment through a combination of biological and physical processes (Bradbury and Snelgrove, 2000). Further understanding of the larval dispersal process is critical for ecological analysis (e.g. migration, feeding, growth, competition and reproduction) and conservation. Recent studies suggest that active swimming directly influences dispersal to appropriate habitat (Ruetz and Jennings, 2000; Leis, 2006), and that dispersal in larval fish is more restricted than previously thought (Cowen *et al.*, 2000; Swearer *et al.*, 1999). Miller *et al.* (1988) showed that prior to settlement, larvae of many species are capable of swimming against currents and can potentially cover large distances (see also Stobutzki and Bellwood, 1994; Leis, 2006).

Most research on fish larval swimming ability has focused on coral reef species and, to a lesser extent, temperate fishes. Reef fish larvae generally appear to be much better swimmers than non-reef fish larvae in comparisons of both short-term and prolonged activity. Settlement-stage reef fish can swim at  $13.5 \text{ cm}\cdot\text{s}^{-1}$  for several days (Stobutzki and Bellwood, 1997), corresponding to  $3\text{--}10 \text{ BL}\cdot\text{s}^{-1}$ . Temperate fish larvae are comparatively poor swimmers, with cruising speeds ranging from  $0.5 \text{ cm}\cdot\text{s}^{-1}$  to  $5 \text{ cm}\cdot\text{s}^{-1}$  ( $1\text{--}3 \text{ bl}\cdot\text{s}^{-1}$ , Blaxter, 1986) when swimming freely in aquaria, but up to  $3 \text{ bl}\cdot\text{s}^{-1}$  in flumes (Houde, 1969; Laurance, 1972; Blaxter, 1986).

Swimming and active habitat selection can contribute significantly to dispersal through advective processes (reviewed by Bradbury and Snelgrove, 2001), especially if competency can be prolonged (McCormick, 1999). For example, model predictions of larval distributions of cod (*Gadus morhua*) were consistent with field observations only when larval behaviour was incorporated (Werner *et al.*, 1993). Thus, good swimming performance can be a critical component of self-recruitment (Leis and Carson-Ewart, 2000), and if fish can “outswim” ambient flow (Leis, 1997; 2006), self-regulation of transport and active habitat selection becomes possible under a greater variety of flow conditions (Leis and Stobutzki, 1999; Bradbury and Snelgrove, 2001). Swimming performance (speed and endurance) can also influence larval feeding rates, energy expenditures, escape reaction from predators, and the extent to which larvae can use active behaviour to modify dispersal, self-recruitment, and

recruitment success (Armsworth, 2001; Sponaugle *et al.*, 2002). Hence, in choosing favourable environments, swimming capability is a central determinant of fitness.

In order to understand the potential importance of active swimming of fish larvae in cold ocean environments, information on swimming ability is needed for different species throughout the entire larval period. Although it is difficult to obtain live individuals in the field of known developmental history, lab rearing provides a means of determining the biological capabilities of larval fishes throughout development from hatch to metamorphosis. By rearing larvae under controlled conditions, it is possible to contrast individuals of known age and history at all developmental stages and to compare swimming ability among species, but acknowledging that performance of wild and reared larvae may be different.

Recently, swimming capabilities have been shown to be influenced by many factors including size, temperature, and study methodology (Stobutzki and Bellwood, 1994). The importance of body size and its influence on physiology, ecology and behaviour of living organisms has long been recognized (Peters, 1983; Miller *et al.*, 1988). Theoretical consideration of development in temperate larval fishes, suggests that size is one of the central factors in survival (Houde, 1989; Pepin, 1991; 1993), and can profoundly affect larval recruitment (Miller *et al.*, 1988). Performance also can change as a function of environmental temperature, which strongly influences larval

development and a host of key morphological characteristics (Hunt von Herbing *et al.*, 1996). Larval size at hatch (Pepin *et al.*, 1997) and development through the larval phase is especially sensitive to temperature change, and even small changes in temperature may substantially decrease larval survival (Green and Fisher, 2004). Moreover, temperature-induced changes in rates of larval morphological development may have indirect effects on swimming performance, because the development of key functional structures such as muscles, gills and biochemical pathways are retarded or accelerated (Taylor *et al.*, 1997). In addition, temperature can strongly influence planktonic duration and thus dispersal potential of marine fish (Bradbury *et al.*, 2000). Cushing (1984) and Atkinson (1996) suggested that reduced temperatures result in longer larval duration and protracted exposure to predators in the high-risk pelagic environment. Temperature is also necessarily linked to viscosity effects on fish larval motion because larvae are small and slow moving in aquatic systems (Podolsky and Emlet, 1993, Fuiman, 1997, Hunt von Herbing, 2002); the effects are especially significant for small larvae in cold water (Gillis, 2003) before they become sufficiently large and fast that swimming motion is inertial rather than viscous.

Three dominant swimming modes have been considered by researchers: (1) sustained swimming speed, (2) critical swimming speed, and (3) burst swimming speed (Beamish, 1978; Hammer, 1995, Plaut, 2001). Critical swim speeds represent an intermediate range (from 30 s to 200 min) between burst (maximum possible) and



sustained swim speeds (maintained for long periods of time), and involves both aerobic and anaerobic energetic pathways. This intermediate measure of swim speed provides an indication of maximum performance for short-term swimming as well as a means of directly comparing swimming capabilities among species and developmental stages.

In order to evaluate the importance of active swimming of larval fish in cold water environments, a better understanding is required of larval swimming ability, and how it is affected by size (age), and temperature. Thus, I examined the development of swimming performance in larvae of two species of larval fish reared at different temperatures. The specific questions addressed were: (1) how does critical swimming speed ( $U_{crit}$ ) change with size and age during larval development, (2) how does  $U_{crit}$  develop at different temperatures in these two species, and (3) how does development of  $U_{crit}$  of larvae compare between pelagic and bottom spawners, noting that the comparison is based on one single species of each that are from different taxonomic orders? Laboratory studies on swimming capabilities of fish larvae may lead to better predictions of larval fish performance under realistic environmental conditions (Bradbury and Snelgrove, 2001), and ultimately the formation of better models to predict recruitment and spatial patterns in fishes.

## **2.2 Materials and Methods**

### *Species selection*

Two cold-water species with contrasting life-history strategies were selected for comparison in this study. Atlantic cod, (*Gadus morhua*), is a pelagic spawner that prefers cool temperature from - 0.5 to 10 °C and, in Newfoundland, spawns from February or March through August (Hutchings *et al.*, 1993). The eggs are buoyant and ~1.5mm in diameter, and the length range of larvae at hatch is typically from 3.3 to 5.7 mm. In contrast, shorthorn sculpin (*Myoxocephalus scorpius*) in Newfoundland spawns on bottom substrate in late November or early December, with larvae hatching in February through April (Scott and Scott, 1988). Spherical eggs are demersal; and the typical larvae length at hatch is 7.4-8.6mm.

#### *Rearing temperature selection*

Larval rearing temperatures were chosen based on field data of seasonal larval concentrations in Placentia Bay, Newfoundland in 1997, 1998 and 1999 (Snelgrove *et al.*, accepted). Ichthyoplankton surveys from April through August indicated that shorthorn sculpin larvae were most abundant in April and persisted through May and June, encompassing near-surface temperatures ranging from 0 to 7 °C. A rearing temperature of  $6 \pm 1$  °C was selected to represent the early summer period whereas  $3 \pm 1$  °C was selected to represent April (spring) temperatures. Cod larvae began to appear in early June with highest abundances in August, encompassing a temperature range of 4 to 10 °C (Snelgrove *et al.*, accepted). A rearing temperature of  $10 \pm 1$  °C was selected to represent summer temperature, whereas  $6 \pm 1$  °C was selected to represent

early summer and to allow a direct comparison between the two species.

### *Culture methods*

#### ***Gadus morhua* (Atlantic cod)**

Fertilized Atlantic cod eggs were acquired in April, 2005 from a naturally spawning captive brood stock at the Ocean Science Center, Memorial University of Newfoundland. Eggs were incubated until hatch at an ambient water temperature of  $\sim 8^{\circ}\text{C}$  which is appropriate for this geographic region. Larvae were transferred to 30 L rearing tanks at a density of  $50 \text{ larvae}\cdot\text{L}^{-1}$  on day 1, with four replicate tanks for each temperature ( $6 \pm 1^{\circ}\text{C}$  and  $10 \pm 1^{\circ}\text{C}$ ). Cultures were maintained at a salinity of  $34.2 \pm 0.1$  psu with 24 h continuous overhead lighting at an intensity of  $\sim 2200$  lux at the water's surface. Light intensity was decreased gradually from 30 days after hatch. Feeding began 3 days post-hatch on a diet of rotifers (*Brachionus plicatilis*) enriched with the protein selco (INVE, Belgium) and microalgae (*Isochrysis* sp.) at a concentration of  $4000 \text{ prey}\cdot\text{L}^{-1}$  (Brown *et al.*, 2003). Feeding was three times daily for the first 40 days at  $10^{\circ}\text{C}$  or 47 days at  $6^{\circ}\text{C}$  (because of the slower development of larvae at this lower temperature, Brown *et al.*, 2003), and then switched to enriched *Artemia* three times daily at a concentration of  $4000 \text{ prey}\cdot\text{L}^{-1}$  until metamorphosis.

#### ***Myoxocephalus scorpius* (shorthorn sculpin)**

Naturally-spawned eggs masses were collected from Logy Bay, Newfoundland in January, 2005, transported to the Ocean Science Center, and incubated at  $3$  or  $6^{\circ}\text{C}$

until hatch. Larvae were transferred to 30 L rearing tanks on day 1 at concentrations of 40 larvae·L<sup>-1</sup>, with two tanks for each temperature treatment (3 and 6 °C). Populations were maintained at a salinity of 34.2 ± 0.1 with 24 h continuous overhead lighting at an intensity of ~2200 lux at the water surface. Feeding began 3 days post-hatch with enriched *Artemia* three times daily at a concentration of 1500 prey·L<sup>-1</sup> until metamorphosis (Brown *et al.*, 2003).

#### *Sample date*

Dates for U<sub>crit</sub> tests were selected based on larval development (total length) and encompassed the time from hatch through larval metamorphosis. The first test was conducted on the first feeding day (typically 3 days post-hatch), and the last tests were run after metamorphosis. Metamorphosis, defined as a series of morphological and physiological changes associated with shifting from a pelagic to demersal existence, was determined based on changes in morphological characters for cod (Table 2.1a, 2.1b), and a combination of morphological character changes and a behavioural shift for sculpin.

#### *Experimental protocol*

For each U<sub>crit</sub> assessment, 10 larvae from each species and temperature were selected haphazardly from replicate tanks, and 1 or 2 larvae per replicate run were transferred to a small (60 ml total volume) Blazka swimming tunnel (Beamish, 1978; Peak *et al.*,

1997), and allowed to acclimate for 10 to 15 minutes under static water conditions. A swim tunnel is a tube through which flow is created via a small impellor connected to a variable speed motor; larval fish are placed in the tube and flow is altered via the impellor to test swimming ability by determining the flow speed at which larvae can no longer maintain their position in the tube. A modified critical swimming velocity ( $U_{crit}$ ) test (Brett, 1964) was then used to determine the potential swimming performance of both species. In this test, current velocity was increased gradually from static, in  $1 \text{ cm}\cdot\text{s}^{-1}$  increments every 2 minutes until the larvae could no longer maintain position for a full 2-minute period. Water velocity in the tunnel was calibrated prior to the addition of fish by using dye injection and high-speed video analysis. The equation used to calculate the  $U_{crit}$  of larvae followed Brett (1964):

$$U_{crit} = U + ((t / t_i) * U_i)$$

Where  $U$  = penultimate speed,

$U_i$  = velocity increment ( $1.0 \text{ cm}\cdot\text{s}^{-1}$ ),

$t$  = time at the final velocity increment (seconds),

$t_i$  = set time interval for each velocity increment (120 seconds)

The estimated error in calculation of critical speed is  $0.0083 \text{ cm}\cdot\text{s}^{-1}$

Ryland (1963) described the transverse velocity gradient in a tube 1.6 cm in diameter, which is similar in size to the tunnel used for this study, and noted that the wall of the

tunnel creates a boundary layer which will reduce the flow speed near the wall because of the drag. This tunnel was operated at a slow speed (less than 10 cm/s), and all the reported swimming speeds were for larvae swimming near the center of the tube to minimise the influence by the boundary layer on fish swimming speed estimation. However, we cannot eliminate the boundary current influence, and the larval swimming speeds reported here might be slightly faster than they would be in the wild.

All tests were performed at ambient light intensities and at water temperatures consistent with rearing temperatures. Fish that exhibited symptoms of stress such as erratic swimming behaviour, lying on the bottom, or clinging to the sides of the swimming tunnel were excluded from the experiments. In some instances, this exclusion reduced sample size from 10 to 8 individuals for a given treatment. Immediately after swim tests, larvae were removed, anaesthetized, measured, and photographed. Measurements included total length, standard length, and body depth. Metamorphosis and settlement was used to mark the end of the larval period.

#### *Data and statistical analyses*

Studies on tropical reef fish larvae (Fisher *et al.*, 2000) and temperate fish larvae (Clark *et al.*, 2005) suggest that  $U_{crit}$  increased with development in a roughly linear manner. Scatter plots and linear regression confirmed the relationship between

swimming ability, age measured as both absolute (days since hatch) age and degree-days, and total length. Degree days is a thermal summation method used to compare individuals raised at different temperatures (Thompson and Riley, 1981) using the formula:

$$\text{Degree days} = \text{Temperature } ^\circ\text{C} * \text{dah (days after hatch)}.$$

For cod, all data points for a given temperature were included in the regression analysis. Although the largest cod individuals in the 10 °C treatment showed initial signs of a morphological shift to a juvenile form, their inclusion in the regression had little effect on the relationship and their behaviour suggested inclusion with the larval period. In the case of shorthorn sculpin, metamorphosis and settlement between larval and juvenile forms were obvious and separate regressions were done for each period.

Reynolds number ( $Re$ ) is the ratio of inertial to viscous forces as an organism moves through water. The Reynolds number was calculated for the mean  $U_{crit}$  of each species at each age using the formula:

$$Re = U_{crit} * L / \nu$$

where  $U_{crit}$  = critical swimming speed ( $\text{m}\cdot\text{s}^{-1}$ )

$L$  = body height (m), corresponding to the cross-sectional width for cod and body length for sculpin, which swims with its body oriented not completely parallel to flow direction, but rather somewhat obliquely.

$\nu$  = kinematic viscosity of seawater ( $\text{m}^2\cdot\text{s}^{-1}$ )

For this calculation,  $v_{3^{\circ}\text{C}} = 1.667 \cdot 10^{-6} \text{ m}^2 \cdot \text{s}^{-1}$ ;  $v_{6^{\circ}\text{C}} = 1.516 \cdot 10^{-6} \text{ m}^2 \cdot \text{s}^{-1}$ ;  $v_{10^{\circ}\text{C}} = 1.346 \cdot 10^{-6} \text{ m}^2 \cdot \text{s}^{-1}$ ; salinity: 34.2 psu.

One way ANOVAs (Analysis of Variance) were used to compare the initial  $U_{\text{crit}}$  and total length at hatch for each species under different rearing temperatures and for the between-species comparison at 6 °C. This comparison contrasted larval swimming ability at hatch for the two species. Because categorical (temperature) and continuous (size and age) explanatory variables were examined, ANCOVAs (Analysis of Covariance) were used to determine whether  $U_{\text{crit}}$  development rates differed within species when differences in total length and water temperature were taken into account. A similar approach was used to determine whether  $U_{\text{crit}}$  development rates differed between the two species at 6 °C and between early pelagic phase before settlement and late larval-early juvenile phase after settlement of sculpin. The assumptions of the model were met by random sampling, utilizing multiple tanks, and distributing multiple egg batches between tanks to minimize interdependence. Data transformation ( $\log_{10}$ ) was used to minimize trends in residuals if not normally distributed.

### 2.3 Results

Experiments were repeated for both species on two separate batches of larvae reared at different times; however, because findings were very similar in statistical analysis for the two batches, results have been simplified to show only one of the larval



batches for each species.

*Temperature effect on larval size and  $U_{crit}$  development*

Critical swimming speed (hereafter swim speed) of cod larvae reared at either 6 or 10 °C increased gradually with larval total length (Fig. 2.1A), and increased proportionally with ( $\log_{10}$  transformed) larval total length (Fig. 2.1B) from the early larval stage to early juvenile stage. Although cod larvae reared at 10 °C hatched at a larger length ( $F_{1,18} = 33.11$ ,  $P < 0.0001$ ) and with a greater swim speed ( $F_{1,18} = 65.85$ ,  $P < 0.0001$ , Table 2.2), and cod larvae at the higher temperature required less time to grow to a given length, swim speeds as a function of total length were similar for both temperatures, with no significant difference between slopes ( $F_{1,16} = 1.35$ ,  $P = 0.27$ , Fig. 2.1B).

Swim speeds of sculpin larvae reared at either 3 or 6 °C also increased with total length (Fig. 2.1C). At 6 °C, swim speed developed quickly from hatch to the settlement stage, and then improved more slowly post-settlement ( $F_{1,7} = 19.53$ ,  $P = 0.007$ ), whereas at 3 °C swim speed improved at a constant rate from hatch to early post-settlement. Swim speed development rates for the two rearing temperatures during the pelagic (pre-settlement) stage were different with respect to total length ( $F_{1,21} = 46.95$ ,  $P < 0.0001$ , Fig. 2.1D). Although the sculpin larvae reared at 3 °C were faster swimmers at hatch than those reared at a higher temperature ( $F_{1,27} = 19.25$ ,  $P < 0.0001$ ), for individuals of a similar length ( $F_{1,27} = 0.21$ ,  $P = 0.65$ ), sculpin larvae

older than 10 days post hatch at 6 °C always swam faster than those reared at 3° C for a given larval length. Metamorphosis and settlement occurred at a length of 13-21 mm at ~24 dah at 6 °C, in contrast to ~72 dah at 3 °C. At settlement, the larvae reared at 3 °C were also faster swimmers ( $F_{1,23} = 21.01$ ,  $P < 0.0001$ ) and larger ( $F_{1,23} = 388.57$ ,  $P < 0.0001$ ) than those reared at 6°C (Table 2.2). Individuals reared at the higher temperature required less time to attain a given length and swimming speeds. Thus, at the higher temperature, the size and speed increases for sculpin were greater but the larval phase was much shorter.

*Comparison between species: Size effect*

At 6 °C swim speed increased with total larval length during the pelagic period for both species. Sculpin hatched with a significantly faster swimming speed and greater total length than cod. The mean critical swimming speed for newly hatched cod larvae was  $1.18 \text{ cm}\cdot\text{s}^{-1}$ , which was significantly slower than the  $5.56 \text{ cm}\cdot\text{s}^{-1}$  measured in sculpin ( $F_{1,26} = 560.24$ ,  $P < 0.0001$ , Table 2.2). The mean total length at hatch was 5.25 mm for cod, which was significantly smaller than the 10.84 mm hatch size for sculpin ( $F_{1,26} = 1737.82$ ,  $P < 0.0001$ , Table 2.2). The rate of development of swim speed with total length for sculpin was significantly greater than for cod in the 6 °C treatment ( $F_{1,13} = 11.71$ ,  $P = 0.007$ ). Although sculpin hatched with a clearly faster swim speed and larger size, cod and sculpin swim speed ranges were similar for a given length. This pattern was evident in plotting measurements of individual sculpin

and cod reared at a common 6 °C temperature (Fig. 2.2A, 2.2B). Swim speeds increased with size at a slower rate as cod larvae developed than for sculpin larvae, but cod eventually attained similar swimming speeds to those seen in sculpin but over a longer time period.

#### *Developmental changes in swim speed*

Critical swimming speed of Atlantic cod larvae increased proportionally with absolute age (days since hatch) and thermal summation age (degree-days) at the two rearing temperatures (Fig. 2.3A, 2.3B). Three days after hatch, mean swim speed ranged from 1.17 cm·s<sup>-1</sup> for larvae reared at 6 °C to 1.93 cm·s<sup>-1</sup> for larvae reared at 10 °C. By the late larval – early juvenile stages, swim speeds ranged from 9.08 cm·s<sup>-1</sup> to 9.7 cm·s<sup>-1</sup> for individuals reared at 6 and 10 °C respectively (Table 2.2). The rates of increase in swim speed with absolute age for different rearing temperatures were similar ( $F_{1,16} = 4.43$ ,  $P = 0.055$ , Fig. 2.3A). However, the development rate of swim speed with thermal summation age at the higher temperature was slower than for the lower rearing temperature ( $F_{1,16} = 512.47$ ,  $P < 0.0001$ , Fig. 2.3B). At a given absolute age and a given thermal summation age less than 170 degree-days, larvae reared at a higher temperature swam faster than larvae at a lower temperature. In other words, larvae reared at a lower temperature required longer time to reach a given swim speed. During the larval stage, for a given age, the size and swim speeds of individuals reared at a higher temperature were consistently greater than for those reared at a lower

temperature (Fig. 2.3A).

Prior to settlement, the swim speed of shorthorn sculpin larvae also increased proportionally with both absolute and thermal summation age at 3 and 6 °C (Figs. 2.3C, 2.3D). On the third day post hatch, swim speed ranged from 5.56 cm·s<sup>-1</sup> for larvae reared at 6 °C to 6.46 cm·s<sup>-1</sup> for larvae reared at 3 °C (Table 2.2). The swim speed at settlement ranged from 9.11 cm·s<sup>-1</sup> to 10.50 cm·s<sup>-1</sup> for individuals reared at 6 and 3 °C respectively (Table 2.2). Initially, larvae reared at 3 °C swam faster than larvae of a similar age reared at 6 °C, however, the rate of increase in swim speed for larvae reared at 6 °C was significantly higher, with a significant difference between slopes comparing absolute age ( $F_{1,21} = 243.49$ ,  $P < 0.0001$ , Fig. 2.3C) and thermal summation age ( $F_{1,21} = 30.86$ ,  $P < 0.0001$ , Fig. 2.3D). Sculpin larvae reared at the lower temperature also took longer to grow to a given length and therefore to attain the swim speed associated with that given length.

#### *Comparison between species: Age effect*

Critical swimming speed increased gradually with both age and with total length for both sculpin and cod larvae before settlement. At hatch, both species had some swimming ability, but swim speed development rate with both absolute age and thermal summation age for sculpin was significantly faster than that for cod in the 6 °C treatment ( $F_{1,13} = 124.41$ ,  $P < 0.0001$ ). Because sculpin hatched at a larger size,

their swim speeds for a given age were greater than those for cod, and it took less development time post-hatch for sculpin to attain a given swim speed.

Reynolds numbers for larvae of both species under different rearing temperatures increased quickly initially and then more slowly as individuals developed from hatch to metamorphosis (Fig. 2.4). Sculpin have larger  $Re$  numbers than cod because of both their larger size and faster swim speed. For cod, numbers were within intermediate or transitional  $Re$  values (20 to 500) as is characteristic of most larval fishes (see Hunt von Herbing, 2002). Cod  $Re$  were lower because of the shorter cross-sectional height as it swims with its body oriented in the horizontal axis parallel to flow direction. For sculpin,  $Re$  values were clearly inertial ( $>200$ , Blaxter, 1986) rather than viscous from an early age because of the longer body length of sculpin and the observation that their body orientation was not parallel to the tunnel or the flow, but instead was consistently oriented at a somewhat oblique angle. Thus, all larval stages of cod were in viscous to transitional flow environments, whereas sculpin larvae were in inertial environments immediately after hatch.

## **2.4 Discussion**

The role of larval fish biology and recruitment patterns in determining population structure has formed the focus for numerous studies (e.g. Doherty, 1987, Leis, 1991a, Stobutzki and Bellwood, 1994). In recent decades, some studies have suggested that larval fishes can actively modify their dispersal and potentially influence recruitment

variation (Blaxter, 1974; Sherman, 1984). Studies that combine active locomotory behaviour, larval duration and physical variables such as water temperature are necessary for improved comprehensive understanding of larval fish distribution patterns.

During the larval stage, shorthorn sculpin and Atlantic cod display significant active locomotive behaviour immediately after hatch, and critical swimming capability increases rapidly with total length, absolute age, and thermal summation age. For shorthorn sculpin, swimming speed improved steadily until metamorphosis, at which point improvements became slower. For Atlantic cod, the transition of swimming speed increase between the late stage larvae and early juveniles was not clearly defined in terms of morphology or in a reduction in the rate at which swim speed improved. Larval fish swimming relies on muscles to generate inertial forces in the surrounding water, and therefore the development of critical swim speed likely depends on growth in morphological characters (body muscles, tail, fins, propulsion area, and undulated body length) that are correlated with fish length and the frequency and amplitude of tail beat (Bainbridge, 1960; Ryland, 1963; Fisher *et al.*, 2000). Other ontogenetic changes in the ability to use available energy reserves and physiological processes (oxygen consumption capability, biochemical pathways) are also important variables. The development of swim speed can be explained in part by the length of the larvae before completing development of swimming-related structures such as fins

and tails. The two species in this study hatched at different sizes, and their swimming ability increased differently with size throughout the larval period. Body length appears to be a basic explanatory variable of larval fish swimming capabilities because it is related to the development of the functional characters larvae use for swimming.

For both of these taxa, and presumably for many other cold water fishes, active behaviour by larvae has the potential to contribute significantly to dispersal, even immediately post-hatch. Although the pelagic spawner (cod) and the bottom spawner (sculpin) in this study hatched larvae of different sizes and different development stages, and swimming in the two species improved at different rates for a given temperature, the range of swim speeds for larvae of comparable sizes were similar between the two species during their pelagic phase. Clark *et al.* (2005) also found no clear dichotomy in performance between similar-sized larvae of temperate pelagic and demersal spawners. Larvae hatched from demersal eggs are usually more developed (Leis and Carson-Ewart, 2002; Leis, 2006), and need less time to begin effective swimming than larvae from pelagic eggs. As a result, larvae from demersal spawners are generally considered to be stronger swimmers; this generality may be true in relation to both age and size. These results suggest a rapid development of critical swimming speed in early larval stages followed by slower development in the later larval stages once a critical milestone has passed for larvae from the demersal spawner.

The transition point was obvious and linked to settlement, possibly because of the habitat shift associated with settlement and locating a suitable habitat. These findings contrast with those on coral reef larval fish (Fisher and Bellwood, 2000), in which the development rate of critical swimming speeds is initially slow in the early larval stage and faster in later stages. This difference may be temperature related.

Individual values of critical swimming speed as a function of larval size (total length) under different rearing temperatures for cod and sculpin suggest that irrespective of temperature, a given length corresponds to a specific swimming speed range (see also Clark *et al.*, 2005). Shorthorn sculpin larvae hatched at a longer length with faster swim speeds than cod, and were more developed in terms of both size and swimming ability than cod for a given age. They also required less time to grow to a given size and associated swim speed, whereas cod eventually attained a similar swim speed range for a given size but over a longer development period.

The relationship between larval size and swim speed is not entirely consistent between cod and sculpin. Limited data on several other species, including rainbow smelt and winter flounder (Fig.2.5, both bottom spawners, Guan unpublished data), suggest that the swim speed – body size relationship can be generalized to some degree when all these species are considered. Indeed the slopes for the rainbow smelt, winter flounder, cod and sculpin are not significantly different ( $F_{1,12} = 10.24$ ,  $P = 0.09$ ) but additional



data from other species are needed. Given their very different life histories it is possible that size may be a broad indicator of swim speeds in cold water marine fishes during their early larval stages. If the pattern holds for other species, it suggests that differences in swimming speed among cold water species are set primarily by size at hatch and the degree to which water temperature influences development (see below) for each species. Enhanced larval dispersal in larvae of pelagic spawners compounds the fully passive dispersal that occurs prior to hatch in pelagic eggs but is absent for demersal eggs that are affixed to the bottom. Given the larger hatch size of eggs from demersal spawners (Thresher 1984) and generally larger larval size of bottom spawners in Newfoundland waters (Snelgrove et al. accepted), this pattern suggests that larvae of bottom spawners may have earlier and more active control on their dispersal during early larval stages compared to pelagic spawners (Table 2.2). Generally, the earlier development of swimming ability and motor skills in larvae of bottom spawners has the capacity to influence dispersal patterns more profoundly through horizontal and vertical movement, and may also broaden the range of environmental conditions under which they can successfully recruit (Snelgrove *et al.* accepted).

Fish are susceptible to temperature change which has potentially significant effects on larval dispersal during development in the pelagic environment (Rombough, 1998). Temperature-induced morphological and muscle-function changes in developing fish

larvae have indirect effects on the development of swimming performance; temperature change also results in changes in planktonic larval duration (PLD) and duration of exposure in the high-risk pelagic environment, and thus the dispersal potential of marine fish (Bradbury *et al.*, 2000, Green and Fisher, 2004). For both species in this study, higher temperature generally resulted in a larger size at hatch and at a given age, shorter larval duration, and shorter development time to achieve a given length and critical swimming speed.

Temperature played an important role in the development rate of swim speed with total length. The effect was especially important for sculpin, in that temperature significantly affected the development rate of critical swimming speed as a function of both age and size. Higher temperatures allowed sculpin larvae to attain a given critical swimming speed and to settle more quickly, but with a smaller size and slower critical swimming speed at settlement. Lower temperatures result in longer pelagic larval duration and delayed metamorphosis, but faster swim speed and larger size at settlement. This pattern suggests an enhanced role for active swimming in late larval stages at low temperature. For pelagic spawning cod, the pattern was less clear in that temperature did not have a significant effect on the development rate of critical swimming speed with size and absolute age. Nonetheless, the significantly faster developmental rate with thermal summation age at the lower rearing temperature suggests that the 6 °C rearing temperature is better for improving swimming

capability over a short time period.

Whether larvae swim in a viscous or an inertial environment has a major effect on their swimming performance because the interaction between larvae and water in viscous environments makes the swimming energetically expensive. Ultimately, this may be the greatest constraint in the development of swimming ability of the very young larvae especially for cold-water species. Cod larvae were in a viscous environment ( $Re < 200$ ) for both temperatures during all larval stages, perhaps explaining the similar development rate of swim speed at different temperatures. Although sculpin larvae also develop in cold water, they effectively swam in an inertial environment because they hatch at higher  $Re$  numbers as a result of their larger size and faster swim speed.

The ecological implication of critical swimming speed relates to the ability of larvae to cover short-distance movement (<500 m) at high speeds and over short time scales (<30 min), and possibly modify broad-scale dispersal patterns via vertical (Job and Bellwood, 2000) or horizontal migration. Vertical migration can play an important role in transport for many marine organisms, and Bakun (1994) suggests that the ocean can be thought as a series of stacked conveyor belts moving in opposite directions. Simply by changing vertical position on small scales in the water column by swimming, and by making use of various currents, horizontal dispersal can also be

controlled by relatively weak-swimming larvae. The advantage of this strategy is that vertical currents tend to be much weaker than horizontal currents, and also the vertical distances are often smaller than horizontal distances, a relatively weak swimmer has a greater chance of regulating its transport through vertical movement than through horizontal swimming, thereby potentially accessing food resources and moving to ideal habitat. In short, successful selection of favourable environmental conditions may be related to the development of critical swimming capability of different marine fish larvae in relation to water temperature.

Larval fish in cold water exhibit critical swimming capabilities that have the potential to influence their dispersion and transport soon after hatch. Swimming improves rapidly through larval development with some slowdown in improvement late in the larval period. However, critical swimming capability is only one aspect of larval biology that can allow fish larvae to influence dispersal (Fisher and Bellwood, 2000). There is a need for more studies on other swimming modes of fish larvae (e.g. sustained swimming), better understanding of when and if directed swimming takes place and under what circumstance, and more studies that integrate swim speed information from laboratory and field studies with physical oceanographic field data to generate models that can predict larval distributions more realistically in the complex marine environment. There is also a need for additional studies to determine whether the size-speed relationship shown here can be extrapolated to a wide range of

marine fish species. Data of this type have the potential to advance significantly the capacity of biophysical predictive models that largely assume passive larval behaviour in predicting the probabilities of dispersal and retention in coastal zones.

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Table 2.1a Morphological character development in cod larvae.

Landmark	Yolk – sac	Fanfold	Paired fins
Stage1: 0–1dah	Large, spherical, full of yolk; >95% yolk remains	Surrounds the whole body including yolk-sac; supracephalic sinus is small, not elevated	Pectoral fins are small, round and well formed
Stage2: 2–3dah	Elliptical and reduced; 70–100% yolk left	Supracephalic sinus is elevated	Simple, round pectoral fins
Stage3: 3–4dah	Yolk-sac reduced; 50–70% yolk left	Supracephalic sinus of the doesal fanfold has reached its maximum elevation	Rounded pectoral fins
Stage4: 6–7dah	Still contains yolk; 25–50% yolk left	Supracephalic sinus maximally elevated	Large cartilaginous base to pectoral fin
Stage5: 8–9dah	Much reduced; 25–50% yolk left	The supracephalic sinus remains elevated	Larger rounded pectoral fins with cartilaginous base
Stage6: 12–13dah	Small sac, 10–25% yolk left	Supracephalic sinus still elevated	Large pectoral fins, cartilaginous base
Stage7: 17–18dah	No yolk left, only remnants of the sac	Supracephalic sinus elevated	Caudal peduncle thickened
Stage8: 25–26dah	Sac remnants	Supracephalic sinus beginning to collapse	Caudal peduncle thickening, base of pectoral fin enlarged
Stage9: 35dah	No remnants visible	Sinus almost collapsed off head	Fin rays in pectoral fins, first caudal fin rays
Stage10: 50dah	No remnants	Caudal fin rays, thickened pectoral fin	Caudal fin rays, thickened pectoral fin
*Stage11: 60dah	No remnants	Sinus collapsed and fanfold covering the trunk; narrower and scalloped at the extreme caudal end	Well formed caudal fin rays, precursors to the dorsal and ventral paired fins present
Stage12: 70dah	None	Not present	Dorsal, anal and pelvic fins are formed but still small, caudal fin is well formed and large

\*late larval-early juvenile stage in this study

Table 2.1b Morphological character development in sculpin larvae.

Landmark	Yolk – sac	Rows on tail	Melanophores
Yolk-sac larvae	Ovoid, unsegmented	Ventral row	Head and trunk
*Post larvae	---	Dorsal and ventral row	Tail (partly), head, trunk and peritoneum

\* stage: settlement completed around 24 dah at 6 °C, and complete around 60 dah at 3 °C

Table 2.2. Mean critical swimming speed and mean total length of Atlantic cod and shorthorn sculpin larvae under different rearing temperatures. Values in parentheses = SE, dah denotes days after hatch (n= 8 to 12 individuals per time period).

	At hatching				Late larval – early juvenile stage		
		3 °C	6 °C	10 °C	3 °C	6 °C	10 °C
Critical swimming speed (cm·s <sup>-1</sup> )	Atlantic cod	-	1.17 (0.07) (3 dah)	1.93 (0.67) (3 dah)	-	9.08 (0.19) (59 dah)	9.70 (0.37) (52 dah)
	Shorthorn sculpin	6.46 (0.14) (3 dah)	5.56 (0.14) (3 dah)	-	10.50 (0.18) (at settlement)	9.11 (0.22) (at settlement)	-
Total Length (cm)	Atlantic cod	-	0.52 (0.01) (3 dah)	0.57 (0.01) (3 dah)	-	1.42 (0.04) (59 dah)	1.89(0.054) (52 dah)
	Shorthorn sculpin	1.05 (0.02) (3 dah)	1.08 (0.01) (3 dah)	-	2.19 (0.03) (at settlement)	1.36 (0.03) (at settlement)	-

Table 2.3. Comparisons of mean critical swimming speed and total length for larvae of four cold water species during the pelagic period. Value in parentheses = SE, dah denotes days after hatch (n= 8 to 12 individuals per time period).

	Species	Winter flounder	Rainbow smelt	Atlantic cod	Shorthorn sculpin
At Hatch	Total Length (cm)	0.54 (0.01)	0.62 (0.01)	0.52 (0.01)	1.084 (0.01)
	U <sub>crit</sub> (cm·s <sup>-1</sup> )	2.07 (0.13)	2.74 (0.11)	1.17 (0.07)	5.56 (0.14)
24 dah	Total Length ( cm )	0.74 (0.01)	_____	0.81 (0.01)	1.36 (0.03)
	Ucrit (cm·s <sup>-1</sup> )	4.95 (0.31)	_____	4.47 (0.16)	9.11 (0.22)
	Status	Larval	Larval	Larval	At Settlement



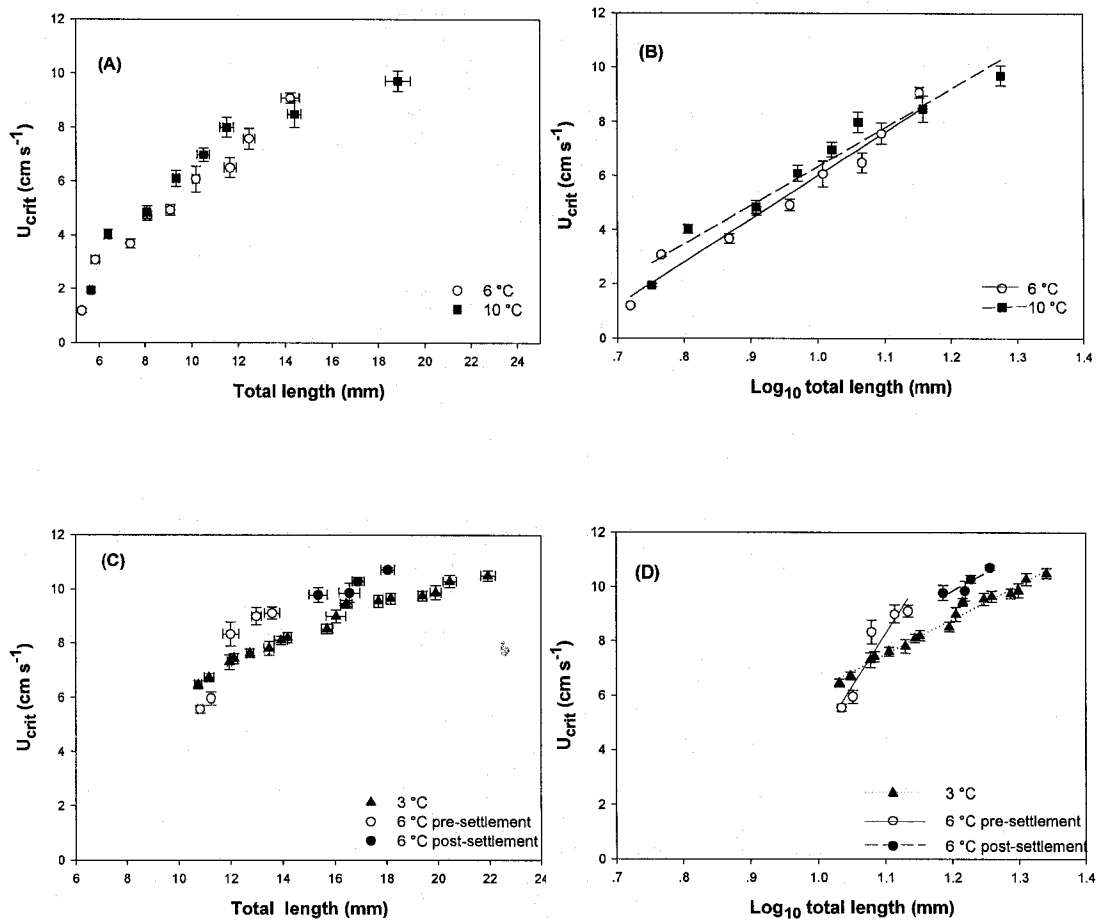


Figure 2.1. Relationship between critical swimming speed and total length under different rearing temperatures. (A) Raw values for cod larvae at 10 °C and 6 °C. (B) Log<sub>10</sub>-transformed cod larvae at 10 °C ( $U_{crit} = 14.35 \cdot \log_{10}TL - 8.01$ ) and 6 °C ( $U_{crit} = 16.01 \cdot \log_{10}TL - 10.00$ ). (C) Raw values for sculpin larvae at 6 °C pre-settlement, 6 °C post-settlement and 3 °C pre-settlement. (D) Log<sub>10</sub>-transformed for sculpin larvae at 6 °C pre-settlement ( $U_{crit} = 39.19 \cdot \log_{10}TL - 34.83$ ), 6 °C post-settlement and 3 °C ( $U_{crit} = 12.88 \cdot \log_{10}TL - 6.65$ ). (n= 8 to 12 individuals per time period).

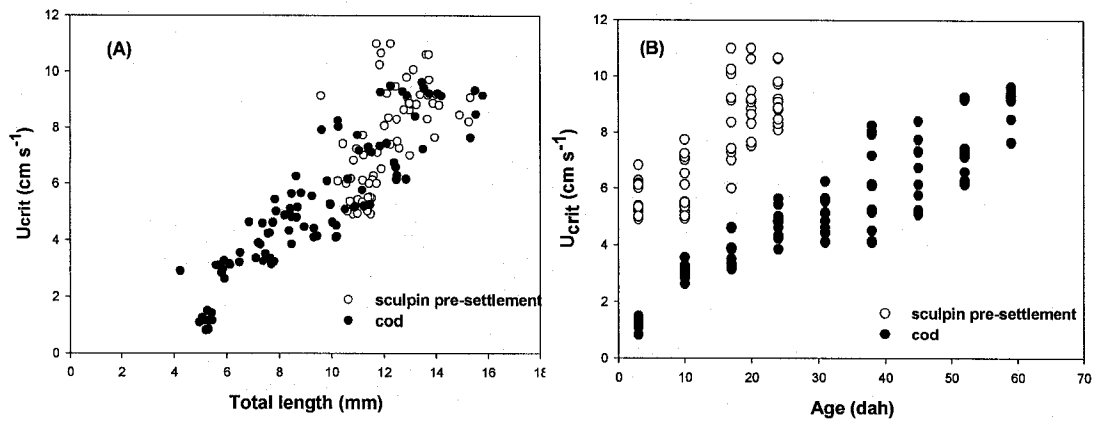


Figure 2.2. Critical swimming speed development during pelagic stages of Atlantic cod and shorthorn sculpin for all individual larvae reared at the same temperature (6 °C). (A) Relationship between critical swimming speed and total length. (B) Relationship between critical swimming speed and absolute age.

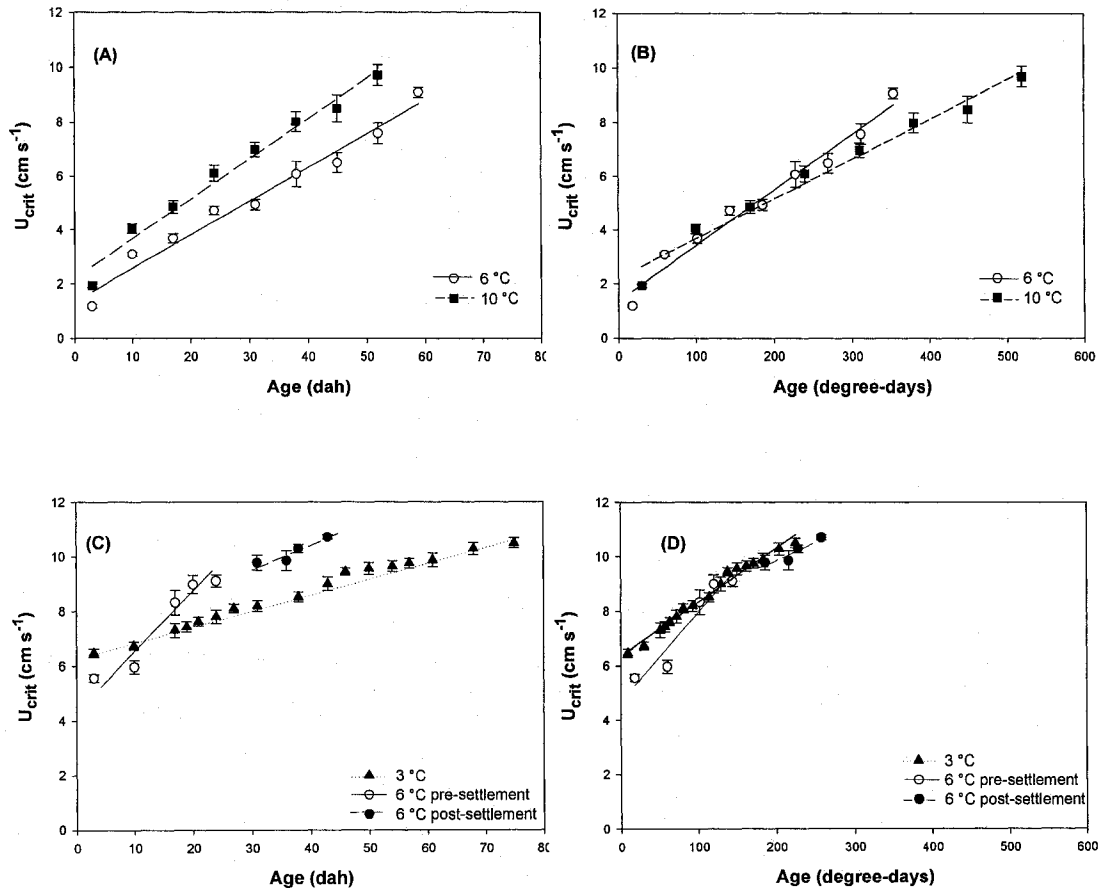


Figure 2.3. Development of critical swimming speed with absolute and thermal summation age under different rearing temperatures. (A) Absolute age for cod larvae (dah, or days after hatch) at 10 °C ( $U_{crit} = 0.15 \text{ dah} + 2.19$ ) or 6 °C ( $U_{crit} = 0.12 \text{ dah} + 1.35$ ). (B) Thermal summation age (degree-days) for cod larvae at 10 °C ( $U_{crit} = 0.01 \cdot \text{degree-days} + 1.35$ ) and 6 °C ( $U_{crit} = 0.02 \text{ degree-days} + 1.35$ ). (C) Absolute age for sculpin larvae during the pelagic period (dah, or days after hatch) at 6 °C pre-settlement ( $U_{crit} = 0.20 \text{ dah} + 4.69$ ), 6 °C post-settlement and 3 °C ( $U_{crit} = 0.059 \text{ dah} + 6.35$ ). (D) Thermal summation age (degree-days) for sculpin larvae (degree-days) at 6 °C pre-settlement ( $U_{crit} = 0.03 \text{ degree-days} + 4.69$ ), 6 °C post-settlement, 3 °C ( $U_{crit} = 0.02 \text{ degree-days} + 6.35$ ). ( $n = 8$  to 12 individuals per time period).

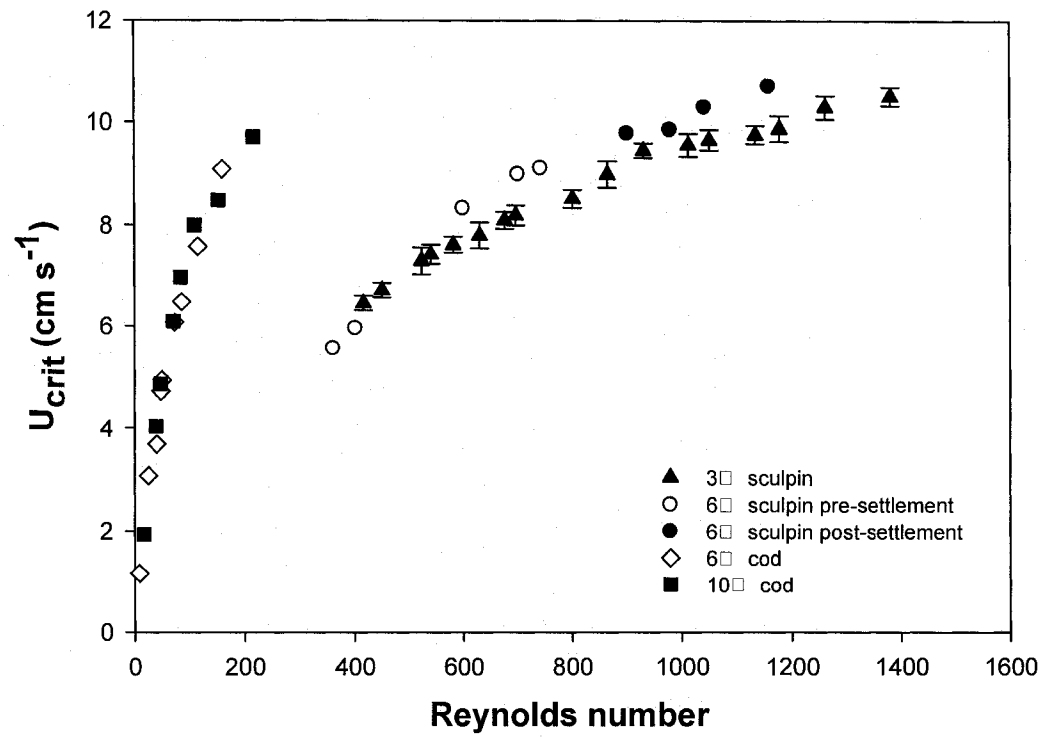


Figure 2.4. Reynolds ( $Re$ ) numbers for Atlantic cod larvae at 6 °C and 10 °C, shorthorn larvae at 3 °C and 6 °C. ( $n= 8$  to 12 individuals per time period).

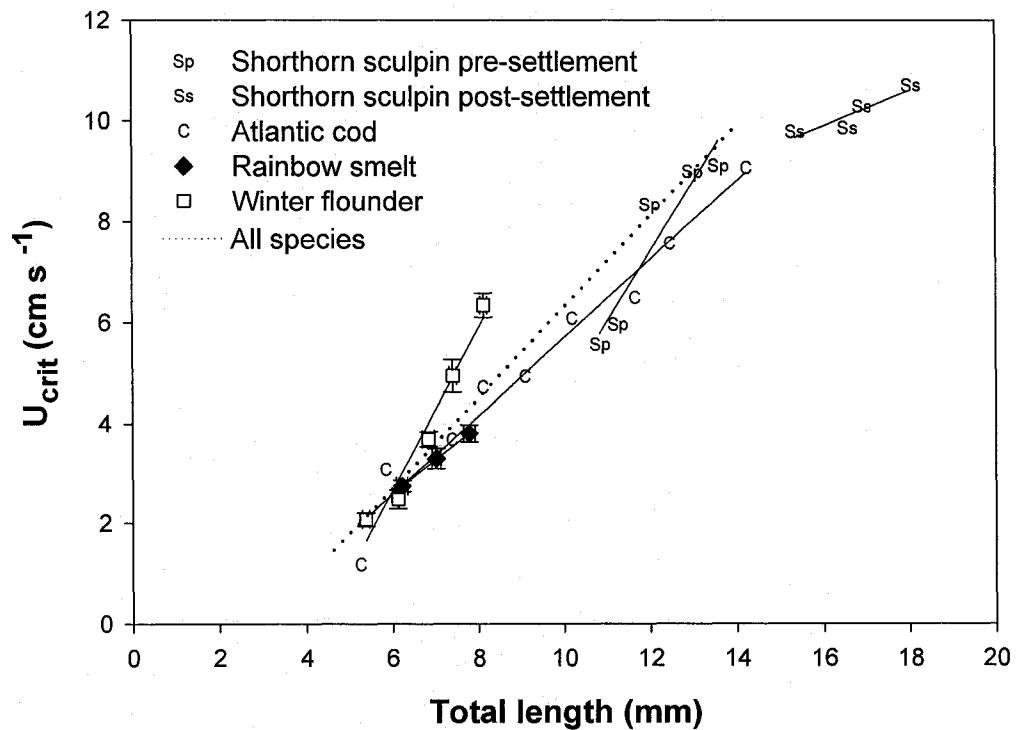


Figure 2.5. Relationship between critical swimming speed and total length for winter flounder ( $U_{crit} = 1.61 \text{ dah} - 7.03$ ) and rainbow smelt (insufficient data on smelt larvae for regression analysis). Values for pre-settlement shorthorn sculpin, post-settlement shorthorn sculpin and Atlantic cod of similar ages are also shown for comparison. An equation showing a general relationship between critical swim speed and total length across species is also shown ( $U_{crit} = 0.79 \text{ dah} - 2.03$ ). ( $n = 8$  to  $12$  individuals per time period).

## **Chapter 3 - Ontogenetic changes in swimming endurance of larvae of two species of cold-water marine fishes and the role of temperature**

### **3.1 Introduction**

Most marine fishes produce larvae that develop in the pelagic realm and therefore disperse some distance before arriving at a suitable juvenile or adult habitat (Dudley *et al.*, 2000). This early dispersal phase is often the only link between spatially isolated adult populations (Sale, 1991), and is likely to influence settlement patterns, subsequent recruitment to fish populations (Leis, 1991a), population dynamics (Dudley *et al.*, 2000) and, ultimately, genetic structure (Burton, 1997). Most marine fish species produce many small offspring that are transported away from spawning and hatching areas on wide-ranging temporal and spatial scales by a complex combination of physical transport mechanisms and active larval behaviour (Sponaugle and Cowen, 1997; Leis, 2006). For these larval stages, arrival at suitable habitat is often essential to completing their life cycle, and the extent to which larvae can control their dispersal is critical (Leis *et al.*, 1996). Larval transport also has important implications for population connectivity and fisheries management (see Sponaugle *et al.*, 2002; Warner and Cowen, 2002).

Several recent studies have shown that passive drift alone cannot explain larval distributions (Leis, 1982; 1991a; Stobutzki and Bellwood, 1997; Leis, 2006) or

settlement patterns, and suggest that swimming ability of larvae plays an important role in the dispersal process as well as recruitment success and self-recruitment (Fisher and Bellwood, 2002). Active swimming in the early larval phase therefore provides a potential mechanism to enhance habitat selection. Most recent studies on larval swimming in fish have focused on coral reef species, and demonstrated that reef fish larvae have impressive swimming abilities (Stobutzki and Bellwood, 1997; Fisher *et al.*, 2000; Leis, 2006) and considerable potential to influence their distributions in the open ocean. Related lab studies on critical swimming capabilities (maximum speeds maintained for 2 minutes) of cold-water larval fishes (Chaper 2) suggest that they also have some capacity to influence their arrival at a suitable settlement location. Late-stage larval reef fish are particularly strong swimmers during their last few days in the pelagic environment (Leis and Carson-Ewart, 1997; Leis, 2006), and larvae of many reef fish species can swim over 100 km in a single bout of up to 10 days at a speed of  $13.5 \text{ cm}\cdot\text{s}^{-1}$  (Stobutzki and Bellwood, 1997). Similar data are currently lacking for cold-water species.

In contrast to critical swimming speed, which is an indication of maximum performance of short-term swimming that utilises both aerobic and anaerobic energetic pathways, sustained swimming ability is largely aerobic and measures maintained swimming activity. It is also a measure of active horizontal swimming behaviour potential during dispersal and long distance migrations. Swimming

behaviours that increase the likelihood of arriving at suitable juvenile habitat will potentially influence the ecology of pelagic larval stages (Stobutzki and Bellwood, 1997) and ultimately geographic distributions (Fisher and Wilson, 2004). Strong swimmers may actively increase or reduce dispersal distances in order to locate suitable juvenile habitat, and swimming also affects encounter rates between predators and prey, thereby influencing growth potential and mortality rates.

The significant advances that have been achieved in reef studies of larval swimming ability have not yet been matched in studies of temperate fish larvae, which so far suggest a weaker but non-trivial role for active behaviour (Hindell *et al.*, 2003). Nonetheless, comprehensive data on swim speeds of temperate and cold-water fish larvae are lacking, as are dispersal models with substantial behavioural components. The general applicability of reef fish results to temperate and cold-water fishes is limited because of the additional complexity added by the influence of temperature change on relatively weak-swimming temperate and cold-water fish (Chapter 2), the seasonal dynamics of temperate and cold-water systems, and the fact that families and orders of fish species often differ in these environments.

Within seasonal environments, differences in size, age, and temperature result in morphological and developmental variability among species and seasons that are likely to influence sustained swimming abilities and dispersal dynamics. Size is a



particularly important determinant of swimming ability (Wardle, 1977; Chapter 2) because it influences thrust, relative swimming speed, muscle mass, and available energy stores. Age usually influences swimming ability directly by determining the larval developmental stage (and therefore size), and the functional capacity of its musculature and locomotory structures. Finally, temperature strongly influences both development and size (Chapter 2), but effects on locomotion are also manifested through physiological performance (e.g. metabolic rate and muscle activity) as well as indirectly by altering the viscosity of the water through which the larvae swim.

In order to evaluate the role that active swimming behaviour plays in the dispersal of larval fish in cold-water environments, I examined development of sustained swimming endurance in two species of larval fish reared at different temperatures. Specifically, I ask: (1) how does sustained swimming endurance change with size and age during larval development, (2) how does sustained swimming endurance develop at different temperatures in different species, (3) how does the development of larval sustained swimming endurance compare between the 2 species examined?

### **3.2 Materials and Methods**

#### *Species selection, temperature selection, and culture protocol*

In order to obtain a more complete understanding of the active swimming behaviour of fish larvae, this work builds on previous studies that examined short-term (critical

swimming speed) swimming potential (Chapter 2) and assesses long-term (sustained swimming time) swimming potential. I also focus on species that were selected to reflect differences in seasonal conditions in coastal Newfoundland and different spawning strategies (see Chapter 2). *Gadus morhua* (Atlantic cod) is a pelagic spawner in spring and summer whereas *Myoxocephalus scorpius* (shorthorn sculpin) is a winter bottom spawner with spring hatching.

Fertilized *Gadus morhua* (Atlantic cod) eggs were acquired in early February 2006 from a naturally spawning captive brood stock. Naturally-spawned *Myoxocephalus scorpius* (shorthorn sculpin) eggs masses were collected from Logy Bay, Newfoundland in January, 2006. Culture methods and rearing duration for the two species are the same as in a related study on critical swimming speeds (Chapter 2) that utilized rearing methods developed by Brown *et al.* (2003). In brief, for sculpin I selected a rearing temperature of  $6 \pm 1$  °C to represent early summer (early June) temperatures and  $3 \pm 1$  °C to represent spring (April) temperatures. For cod, I selected a rearing temperature of  $10 \pm 1$  °C to represent summer (late June) temperatures, and  $6 \pm 1$  °C to represent early summer conditions and to allow a direct comparison between the two species. These temperatures are typical for times of year when these larvae occur in coastal Newfoundland (Snelgrove *et al.*, accepted).

For cod, sustained swim speed tests were initiated immediately after hatch and

repeated approximately once every week until the late larval stage, whereas for sculpin, tests were conducted immediately after hatch and at three-day intervals until metamorphosis and settlement, as described in Chapter 2. Tests were performed at ages and time intervals that corresponded with earlier experiments on critical swim speeds in order to allow for direct comparisons between studies. At least 10 larvae were tested at each temperature (3, 6 or 10 °C) for each species and swimming trial, with 1 or 2 larvae in the swim tunnel at once for any one replicate test run.

#### *Experimental protocol*

The measurement of swimming endurance of larvae until exhaustion at a specific current velocity (hereafter swimming ability or time) is a standard measure of long-term sustained swimming performance that can aid in evaluation of larval fish dispersal (Stobutzki and Bellwood, 1997). For each swimming ability assessment trial, larvae from each species and temperature were selected haphazardly from replicate tanks, carefully transferred to a 60 ml-Blazka swimming tunnel (Beamish, 1978; Peak *et al.*, 1997; also see Chapter 2), and allowed to acclimate for 10 to 15 minutes in static flow conditions ( $0 \text{ cm}\cdot\text{s}^{-1}$ ). Water flow speed was then increased slowly to a test speed of  $10 \text{ cm}\cdot\text{s}^{-1}$  over a period of 2 min. Larvae were observed continuously, recording the total swim time until fatigue; fatigue was indicated by fish that were unable to maintain position in the flow and were swept into the mesh at the downstream end of the swim tunnel. A flow speed of  $10 \text{ cm}\cdot\text{s}^{-1}$  was selected to

approximate mean surface current speeds in the Newfoundland coastal marine environment (Fig. 8 in Bradbury *et al.*, 2003). All tests were conducted during the daytime hours at ambient light intensities (diffuse, overhead fluorescent lights in a windowless room), and at water temperatures consistent with each rearing temperature. Fish were not fed immediately before or during the swimming trials, and individuals that exhibited symptoms of stress such as erratic swimming behaviour, lying on the bottom, or clinging to the sides or surface of the swimming tunnel were excluded from the analyses. In some instances this exclusion reduced sample size to as few as 8 larvae per trial. All of the swimming times reported here were for larvae swimming near the center of the tube, thus minimising bias associated with fish swimming in the reduced flow of the tube boundary layer. Larvae were removed, anaesthetized, measured, and photographed immediately after swim tests. Size measurements included total length, standard length, body depth, and wet weight; however, analyses reported here focus on total length.

#### *Data and statistical analyses*

Studies on tropical reef (Fisher *et al.*, 2000; 2002) and temperate (Clark *et al.*, 2005) fish larvae suggest that sustained swimming ability increases with development in a roughly exponential manner. Scatter plots and linear regressions were used to investigate the relationship between sustained swimming time and sustained swimming distance with total length and age, where age was measured as both

absolute (days since hatch) age and degree-days. Swimming distance was calculated from sustained swimming time using the formula:

$$\text{Swimming distance (km)} = \text{Sustained swimming time (s)} * 10 \text{ cm} \cdot \text{s}^{-1} * 10^{-5} \text{ km} \cdot \text{cm}^{-1}$$

Degree-days is a thermal summation method used to compare individuals raised at different temperatures (Thompson and Riley, 1981), and was calculated as:

$$\text{Degree-days} = \text{Temperature } ^\circ\text{C} * \text{dah (days after hatch)}$$

For cod, all data for a given temperature were used for the regression analysis. Although the largest cod individuals in the 10 °C treatment displayed initial signs of a morphological shift to a juvenile form, their inclusion in the regression had little effect on the linear relationship, suggesting inclusion with the larval period. In the case of shorthorn sculpin, metamorphosis and habitat shifts between larval and juvenile forms were obvious and separate regressions were done for each developmental phase.

Reynolds number (*Re*) is the ratio of inertial to viscous forces as an organism moves in water. In this study, Reynolds number was calculated with the flow speed 10 cm·s<sup>-1</sup> at each age using the formula:

$$Re = U * L / \nu$$

where  $U$  = swimming speed, which is equal to flow speed ( $10 \text{ cm}\cdot\text{s}^{-1}$ ) in this study

$L$  = body height (m), defined as cross-sectional height for cod and body total length for sculpin, which swims with its body oriented obliquely to the flow direction

$\nu$  = kinematic viscosity of seawater ( $\text{m}^2\cdot\text{s}^{-1}$ )

For this calculation,  $\nu_{3^\circ\text{C}} = 1.667 \cdot 10^{-6} \text{ m}^2\text{s}^{-1}$ ;  $\nu_{6^\circ\text{C}} = 1.516 \cdot 10^{-6} \text{ m}^2\text{s}^{-1}$ ;  $\nu_{10^\circ\text{C}} = 1.346 \cdot 10^{-6} \text{ m}^2\text{s}^{-1}$ ; salinity = 32 psu. Scatter plots were also used to investigate the relationship between sustained swim time, swimming distance, and Reynolds number.

One way ANOVAs (Analysis of Variance) compared mean swim time (and thus mean swimming distance) at hatch and settlement, and mean total length at hatch for each species under different rearing temperatures. An additional ANOVA compared these variables between species for the common  $6^\circ\text{C}$  treatment. ANCOVAs (Analysis of Covariance) were used to examine whether size and water temperature influence the development of sustained swimming ability, and whether swimming development rates differed between the two species at  $6^\circ\text{C}$ . Model assumptions were met by random sampling of multiple tanks, and distributing multiple egg batches among tanks

to minimize interdependence. Data transformation ( $\log_{10}$ -transformation) minimized trends in residuals in instances where data were not normally distributed.

### 3.3 Results

#### *Effect of temperature on larval size and sustained swimming ability*

Swimming endurance (and swimming distance) of cod larvae reared at either 6 or 10 °C increased exponentially with total increase in larval length (Fig. 3.1A) which is slow during the early larval phase before increasing quickly from the late larval to early juvenile phase. Swimming endurance also increased linearly with  $\log_{10}$  transformed swimming ability (Fig. 3.1B). Larvae reared at 6 and 10 °C hatched at a similar length ( $F_{1,19} = 1$ ,  $P = 0.33$ ), and for neither treatment did larvae exhibit any sustained swimming ability at hatch (Table 3.1). Larvae at 10 °C began to show limited swimming ability (0.9 s of sustained swimming time, corresponding swimming distance of  $4.0 \times 10^{-5}$  km,  $t_{1,18} = -3.857$ ,  $P = 0.001$ ) at a body length of 6.6 mm. This milestone occurred at an earlier age than in larvae reared at 6 °C (1.4 s swim time, corresponding swimming distance of  $1.4 \times 10^{-4}$  km,  $t_{1,18} = -3.279$ ,  $P = 0.004$ ) at a body length of 7.6 mm. By the late larval / early juvenile phase around 52 days after hatch, swim time and swimming distance for 6 °C treatments ranged from 14.9 s and  $1.5 \times 10^{-3}$  km (total length of 10.3 mm) to 56.2 s and  $5.6 \times 10^{-3}$  km for 10 °C treatments (total length of 15.3 mm, Table 3.1). Sustained swim time ( $\log_{10}$  transformed) or swimming distance ( $\log_{10}$  transformed) as functions of total length were different at the two different temperatures, with faster development at the lower

temperature ( $F_{1,10} = 5.60$ ,  $P = 0.05$  and  $F_{1,10} = 1.53$ ,  $P = 0.256$  respectively). Generally, prior to metamorphosis, larvae at a higher temperature required less time to grow to a given sustained swim time, and to cover a given swim distance, but swimming endurance was stronger for individuals reared at a lower temperature than larvae of a similar size from the higher temperature after the first week after hatch.

Sustained swimming time and swimming distance of sculpin larvae reared at either 3 or 6 °C also increased with total length (Fig. 3.1C). At 6 °C, time and swimming distance increased gradually from values at hatch (21.5 s and  $2.2 \times 10^{-3}$  km respectively) until just before settlement, where values were 69.9 s and 0.00699 km respectively. However, swimming ability improved more quickly after settlement ( $F_{1,7} = 22.26$ ,  $P = 0.009$ ). At 3 °C, swim time and swimming distance improved steadily with larval length from values at hatch of 4.6 s and 0.00046 km respectively to pre-settlement values of 92.7 s and  $9.3 \times 10^{-3}$  km. During the pelagic (pre-settlement) phase, development rates of swimming time and swimming distance at different rearing temperatures were similar with respect to total length ( $F_{1,14} = 0.42$ ,  $P = 0.528$ ). At hatch, larvae reared at 3 °C were significantly weaker swimmers than those reared at a higher temperature ( $t_{1,18} = 23.61$ ,  $P = 0.001$ , Table 3.1 ) and were smaller in size. Larvae reared at 6 °C generally swam longer (and thus further) than those reared at 3 °C at a given larval size. Metamorphosis and settlement occurred at a length of 13.8 mm on day 24 at 6 °C, which differed markedly from larvae at 3 °C, which settled on



day 52 at 15.4 mm. At settlement, compared to larvae reared at 6 °C, individuals reared at 3 °C were larger ( $t_{1,18} = -4.909$ ,  $P = 0.0001$ ), but with similar sustained swimming time ( $t_{1,18} = -1.409$ ,  $P = 0.176$ , Table 3.1). Generally, individuals reared at the higher temperature required less time to attain a given developmental stage, total length, sustained swimming time, and swimming distance.

Sustained swimming ability increased with larval size during the pelagic period at 6 °C for both species. At hatch, sustained swimming time and distance for newly hatched cod larvae were both 0 at 4.67 mm length compared to a significantly longer time (21.5 s) and distance (0.002 km) of 11.02 mm in sculpin ( $t_{1,18} = 1.56$ ,  $P < 0.001$ , Table 3.1). The increase rate of sustained swim endurance (time and swimming distance,  $\log_{10}$  transformed) with length for cod was significant faster than sculpin ( $F_{1,12} = 130.25$ ,  $P < 0.05$  and  $F_{1,12} = 840.11$ ,  $P < 0.05$ ).

#### *Developmental changes in sustained swimming abilities (absolute age)*

Sustained swimming time and swimming distance of Atlantic cod larvae increased exponentially with absolute age (days since hatch) at the two rearing temperatures (Fig. 3.2A). Although larvae reared at either temperature had no sustained swimming ability at hatch, larvae at 10 °C began to show swimming ability at an earlier age (17 dah,  $t_{1,18} = -3.857$ ,  $P = 0.001$ ) than larvae at 6 °C (24 dah,  $t_{1,18} = -3.279$ ,  $P = 0.004$ ). By the late larval / early juvenile stages (~ 52 dah), individuals reared at 10 °C were

significantly stronger swimmers than individuals at 6 °C (Table 3.1). Temperature had no significant effect on improvement rate in swimming ability as a function of absolute age ( $F_{1,10} = 0.8$ ,  $P = 0.402$ , Fig. 3.2B). However, at a given absolute age, larvae reared at the higher temperature could swim longer and farther than larvae reared at the lower temperature. In other words, larvae reared at a lower temperature required longer to reach a given swimming ability and swim distance at  $10 \text{ cm}\cdot\text{s}^{-1}$ .

Sustained swimming ability of shorthorn sculpin larvae also increased as a function of absolute age (days since hatch) for the two rearing temperatures prior to settlement (Fig. 3.2C), as did swimming distance. At 3 days after hatch, larvae reared at 6 °C were stronger swimmers (swim time = 21.5 s, swimming distance =  $2.2 \times 10^{-3}$  km) than individuals reared at 3 °C (4.6 s and  $4.6 \times 10^{-4}$  km,  $t_{1,18} = 4.859$ ,  $P = 0.0001$ ). Throughout the pelagic larval phase, swim time and distance also increased at a faster rate for larvae reared at 6 °C ( $F_{1,14} = 6.28$ ,  $P = 0.029$ ). Larvae reared at 6 °C that could only swim for 69.9 s (or  $6.7 \times 10^{-3}$  km) at settlement ~ 24 dah. Larvae reared at 3 °C could swim for a similar duration 92.7 s (or  $9.3 \times 10^{-3}$  km) at settlement ~52 dah ( $t_{1,18} = 1.4090$ ,  $P = 0.176$ , Fig. 3.2D, & Table 3.1). During the larval phase, at a given absolute age, larvae reared at a higher temperature swam longer and further than larvae reared at a lower temperature, and also developed and settled faster.

The development rate of swim time ( $\log_{10}$  transformed) with absolute age for cod was

significantly faster than that for sculpin at 6 °C ( $F_{1,9} = 187.53$ ,  $P < 0.0001$  and  $F_{1,12} = 74.86$ ,  $P < 0.005$ ). Sustained swimming ability in cod improved little throughout the whole larval pelagic phase, and because sculpin hatched at a larger size although developed at a slower rate, their swim endurance for a given age were consistently greater than those for cod.

*Developmental changes in sustained swimming abilities (degree-day)*

Sustained swimming endurance increased exponentially in relation to degree-days, and was well described by a log-linear model (Fig. 3.3A). Cod larvae at 6 °C began to show sustained swimming ability 144 degree-days ( $t_{1,18} = -3.279$ ,  $P = 0.004$ ) after hatch, in contrast to the 170 degree days ( $t_{1,18} = -3.851$ ,  $P = 0.001$ ) required by larvae reared at 10 °C. Swim time (and swimming distance) increased with thermal summation age at a similar rate for the two rearing temperatures, with no significant difference between slopes ( $F_{1,10} = 0.8$ ,  $P = 0.402$ ). During the larval phase, for a given thermal summation age, the sustained swimming time and swimming distance of individuals reared at a lower temperature were consistently greater than individuals reared at the higher temperature.

Different rearing temperatures did not affect sustained swimming ability improvement in sculpin larvae with respect to thermal summation age (degree-days) ( $F_{1,14} = 4.37$ ,  $P = 0.061$ , Fig. 3.3C). In fact, development of swimming ability correlates with thermal

summation age rather than absolute age, and “older” larvae based on thermal summation age generally have stronger swimming ability. Larvae reared at 6 °C had longer swim time at 18 degree-days than 9 degree-days larvae at 3 °C. At settlement, 3 °C larvae were older in absolute age (longer pelagic larval duration), but younger in thermal summation age than larvae reared at 6 °C (144 degree-days versus 156 degree-days). Similarly, swimming distance increased with thermal summation age and, like cod larvae, individuals reared at a higher temperature consistently swam for a shorter time and distance than larvae at a lower temperature at a given thermal summation age.

In comparing the two species at 6 °C, the development rate of time and swimming distance ( $\log_{10}$  transformed) with thermal summation age for cod was also significantly greater than that for sculpin ( $F_{1,9} = 187.53$ ,  $P < 0.0001$ ). Because sculpin hatched at a larger, more developed stage, their swim endurance for a given age were always greater than those for cod even with the slower development rate, and sculpin took less time to reach a given sustained swimming ability.

Sustained swimming time increased with Reynolds ( $Re$ ) number from hatch to metamorphosis in both species irrespective of temperature (Fig. 3.4 A & B), but the trajectory of the increase differed. Sculpin had larger  $Re$  and stronger sustained swimming ability than cod from hatch onward because of their larger size. Cod larvae

had limited sustained swimming ability during any of the pelagic phase, with  $Re < 200$  or within the transitional range of 20 to 500 that is characteristic of most larval fishes (see Hunt von Herbing, 2002). The shorter cross-sectional height of cod larvae, which swim with the long axis of their body oriented parallel to flow direction contributes to lower  $Re$ . In contrast,  $Re$  were clearly inertial rather than viscous from an early age for sculpin because of their longer body length and body orientation which was oblique to flow direction when swimming. Thus, all cod larval stages were viscous to transitional, whereas sculpin larvae were inertial swimmers immediately after hatch.

### **3.4 Discussion**

Understanding how organisms move in the context of their environments is fundamental to understanding their ecology (Armstrong, 2001). The majority of marine fish possess a pelagic phase that is critical to their population dynamics and population connectivity (see Sponaugle et al., 2002; Warner and Cowen, 2002). During this stage, larval transport to a suitable settlement habitat is believed to be an interactive process that is affected by hydrography (e.g. Pepin *et al.*, 1995) and active swimming behaviour (e.g. Leis *et al.*, 1997; 2000). The identification of biological as well as physical mechanisms that contribute to larval transport in marine fishes is now recognized as a critical area of research for marine ecology, conservation, and management. (e.g. Cowen *et al.*, 2000).

Sustained swimming ability can modify larval dispersal and define the relative importance of active horizontal control and passive mechanisms (Fisher and Bellwood, 2002); competent swimmers may be able to contribute to field distributions whereas dispersal in weaker-swimming species may be controlled primarily by hydrology. Sustained swimming ability is also linked to mortality levels because it influences predator and prey encounter rates. Recent flume-based, sustained swimming experiments have provided a performance measure of the maximum long-term swimming abilities of larvae, and thus their potential to contribute to dispersal over extended periods of time (Fisher and Bellwood, 2001). Data from sustained swimming studies have already been incorporated into models that examine the effect of behaviour on larval dispersal (Armsworth, 2001), and it is becoming increasingly important to obtain reliable estimates of swimming abilities of larvae.

*Development of sustained swimming ability: Size and age effects*

The pelagic (cod) and bottom (sculpin) spawners investigated in this study displayed very different sustained swimming ability immediately after hatch, and also improved quite differently as a function of absolute age, thermal summation age, and size. For the early pelagic phase of cod, larval sustained swimming ability was absent or very weak, then started to increase during the late larval phase, whereas sustained swimming ability in sculpin larvae improved steadily prior to settlement, and then improved very rapidly after metamorphosis and the accompanying habitat shift. These

between-species differences suggest that sustained swimming ability development is dependent on size-related physiological, morphological and behavioural changes during ontogeny. The weaker swimming endurance of cod is consistent with the limited swimming capabilities exhibited from hatch through metamorphosis and appears to be a general characteristic of this species. In studies on tropical coral reef fish, Stobuzki and Bellwood (1997) suggested that larvae of some species can swim at  $13.5 \text{ cm}\cdot\text{s}^{-1}$  over 100 km in a single bout over a time period of 10 days, and the sustained swimming times of 16 to 26 hours at settlement size suggested for temperate fish (Clark, 2005); both studies suggest much greater swimming endurance compared to the cold-water species examined here.

As was observed with critical swimming speed (Chapter 2), the development of sustained swimming ability of both species differs markedly through the pelagic larval phase. In sculpin, swim time increased steadily from hatch until settlement, followed by a rapid increase after settlement, whereas for cod larvae, swim time improved only slightly during the entire pre-flexion phase. As was observed with critical swimming speed, there was a clear transition at settlement for sculpin. A sharp improvement in swimming capability following notochord flexion and formation of the caudal fin has also been described in tropical (Fisher et al., 2000; Leis, 2006) and temperate (Clark *et al.*, 2005) fish larvae. For ecologists, this transition from a pre- to post-settlement stage is important because it leads to a more fixed phenotype and physiology with

respect to active locomotion (Balon, 1999). With increased size and age, fish typically have better developed musculature and locomotory structures (Stobutzki and Bellwood, 1997). Greater metabolic reserves are expected, and a slower relative speed in bigger fish also requires relatively less swimming effort. All of these factors contribute to the accelerated development rate of swimming endurance in the late larval phase.

The larvae of sculpin, a bottom spawner, were more developed and larger at hatch, and possessed stronger sustained swimming ability and larger size than cod, the pelagic spawner. This difference, in tandem with substantial egg dispersal in pelagic spawners (e.g. Bradbury *et al.*, 2000), results in a much greater potential for active behaviour to contribute significantly to dispersal in bottom spawners. Sculpin larvae were more developed in swim endurance for a given age although they developed at a significantly slower rate than cod. As with critical swimming speed (Chapter 2), sculpin display a sharp improvement in sustained swimming ability at settlement, in contrast to a more gradual increase in cod during the late larval-early juvenile phase. Generally, larvae from bottom spawners in Newfoundland waters are larger than those from pelagic spawners (Snelgrove *et al.*, accepted) suggesting that larvae of bottom spawners may have greater potential to influence dispersal during early larval stages than pelagic spawners. The earlier development of strong swimming ability and motor skills in larvae from bottom spawners has the capacity to influence dispersal patterns



through horizontal movement, and may also broaden the range of environmental conditions under which they may recruit (Snelgrove *et al.*, accepted).

*Development of sustained swimming ability: temperature effects*

Temperature plays a critical role in the development and dispersal of early life history stages by affecting stage duration (Bradbury *et al.*, 2001). It also influences development stage at hatch, muscle function and physiological and morphological development rate, all of which could contribute to larval dispersal. In this study, higher temperature generally resulted in a larger size at a given absolute age, earlier evidence of sustained swimming behaviour, and shorter larval duration. Nonetheless, for sculpin in this study, higher temperature led to a faster increase rate in swimming endurance as a function of absolute age but not as a function of thermal summation age or total length. In cod, the effect of temperature on the development of sustained swimming ability as a function of size was significantly different; however as a function of age it was not. The faster development of swimming endurance observed at the lower temperature was surprising.

In seasonal environments, larvae could potentially disperse in comparatively warm (summer) or cold (spring) temperatures. At warmer temperatures, larvae display stronger swimming ability at a given absolute age and have a shorter pelagic duration. Thus, they have comparatively strong active control, whereas at lower temperatures

larvae would be expected to be relatively weaker swimmers that require more time to reach a given developmental stage or metamorphosis, but with a similar swimming ability at that time. This convergence may help to offset the indirect effects of temperature on dispersal. The same pattern is seen in development of critical swimming speed (Chapter 2), where temperature affects the length of time to develop to a given size and swimming ability. However, additional data are needed for other cold-water species in order to determine the generality of this relationship.

Reynolds ( $Re$ ) number is also important in understanding the development of larval fish swimming ability. Cod larvae were in a viscous environment ( $Re < 250$ ) for both temperatures during the entire larval phase, making swimming energetically expensive. Fisher et al. (2000) showed that coral reef fish do not develop substantial sustained swimming until  $Re$  values are considerably larger than 200. For cod, even late larvae-early juveniles had a  $Re$  less than 200. Thus, one possible explanation for the similar development rates of swim endurance of cod larvae at different temperatures in this study may be that the effect of viscosity in cold water for very small larvae swamped any temperature effects on swim time increase.

Our results demonstrate that, for the species tested, cold-water fish larvae are poor swimmers compared to temperate and tropical fish larvae. In this study, sculpin and cod larvae were not fed and did not rest within each of the trials; however, it is very

unlikely that larvae would swim until exhaustion without feeding in the sea (Leis, 2006). If larvae can fuel their swimming by feeding while swimming, then laboratory values of endurance using unfed larvae will be underestimated (Fisher and Bellwood, 2001; Leis and Clark, 2005; Leis 2006). Clearly, field verification of these findings is necessary.

#### *Implications for dispersal of demersal and pelagic species*

Bottom and pelagic spawners have different dispersal potentials. The behaviour of species with planktonic eggs may have less active influence on dispersal compared to bottom spawning taxa because they tend to be smaller and less developed at hatch, but have a relatively longer pelagic larval phase (Thresher, 1991). For these pelagic species, physical forces are likely to predominate in dispersal patterns over behaviour in the first few days after hatching. However, comparable (this study) or greater (Fisher & Bellwood, 2002) swimming ability at settlement of species with pelagic eggs in comparison with bottom spawners may help offset their slower rate of development, so that active behaviour may influence dispersal patterns, albeit at a later developmental stage.

There is increasing evidence that reef fish larvae can actively locate suitable areas for settlement (Swearer *et al.*, 1999). The data presented here demonstrate that the two species of cold-water fish larvae that were examined are weak swimmers compared to

coral reef fish, in that they are capable of swimming against currents only for a short time period, and therefore for potentially limited distances. Sustained swimming ability is a major determinant of active, directed horizontal movement by larvae, whereas critical swim speed is more important for relatively short movement to select flow speeds associated with specific depths (e.g. vertical migration, Fisher *et al.*, 2000). Nonetheless, both behaviours can have substantial ramifications for pelagic larval fish transport.

An improved understanding of larval fish dispersal will require that active swimming behaviour and physical transport mechanism are both taken into account. For cold-water species, shorthorn sculpin are strong swimmers immediately after hatch, and are potentially able to make efficient use of motor skills for dispersal at an early developmental stage. For pelagic spawning cod, larvae are relative passive and presumably have less active control on early transport during their pelagic larval phase. Nonetheless, sustained and critical swimming capabilities are only two aspects of larval behaviour that can influence dispersal. There are several other important aspects that remain to be addressed. The role of vertical movement, importance of variation among individuals and species, and an evaluation of the orientation abilities of the pelagic stages are all important considerations. Finally, there is a clear need to validate the extent to which these laboratory-based studies are realized in the field.

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Table 3.1. Mean (and SE) sustained swimming endurance and total length of Atlantic cod and shorthorn sculpin larvae for different rearing temperatures. Values in parentheses = SE, dah denotes days after hatch (n = 8 to 12 individuals per time period).

		At hatching (3 dah)			Early juv. stage (cod: 52 dah, sculpin: at settlement)		
		3 °C	6 °C	10 °C	3 °C	6 °C	10 °C
Sustained swimming Time (s)	Atlantic cod	-	0	0	-	14.9 (10.8)	56.2 (17.5)
	Shorthorn sculpin	4.6 (3.7)	21.5 (10.4)	-	92.7 (36.1)	69.9 (36.3)	-
Sustained travel Distance (km)	Atlantic cod	-	0	0	-	0.002 (0.001)	0.006 (0.002)
	Shorthorn sculpin	0.0005 (0.0004)	0.002 (0.001)	-	0.009 (0.004)	0.007 (0.004)	-
Total Length (mm)	Atlantic cod	-	4.6 (0.2)	4.7 (0.4)	-	10.3 (0.5)	15.3 (1.7)
	Shorthorn sculpin	10.76 (0.29)	11.02 (0.33)	-	15.42 (0.83)	13.76 (0.68)	-

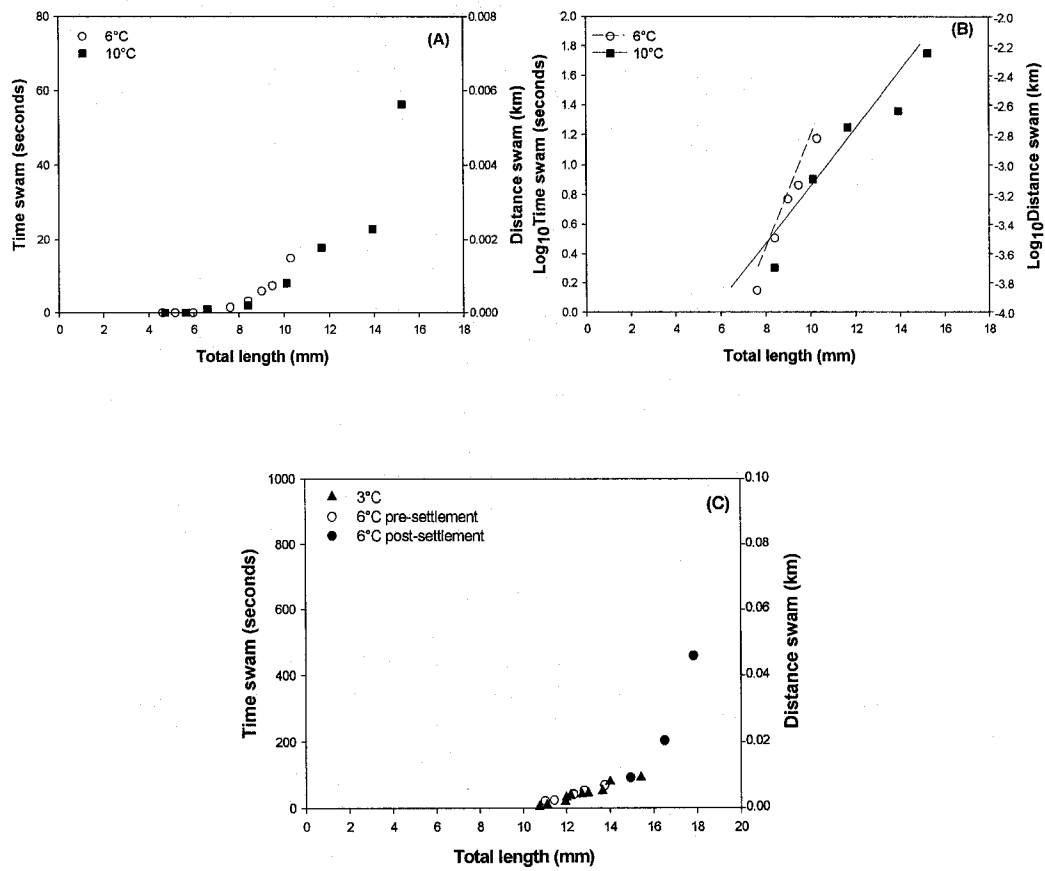


Figure 3.1. Relationship between sustained swimming time (seconds), swimming distance (km) and total length for different rearing temperatures. (A) Non-transformed values for cod larvae at 10 °C and 6 °C, (B) Log<sub>10</sub>-transformed cod larvae at 10 °C ( $\text{Log}_{10} \text{ Time} = -1.300 + 0.2010 \text{ Total length}$ ,  $\text{Log}_{10} \text{ Distance} = -5.670 + 0.2300 \text{ Total length}$ ) and 6 °C ( $\text{Log}_{10} \text{ Time} = -2.690 + 0.3780 \text{ Total length}$ ,  $\text{Log}_{10} \text{ Distance} = -6.690 + 0.3780 \text{ Total length}$ ), (C) Non-transformed values for sculpin larvae at 6 °C pre-settlement ( $\text{Time} = -182.0 + 18.300 \text{ Total length}$ ,  $\text{Distance} = -1.820 + 0.1830 \text{ Total length}$ ), 6 °C post-settlement and 3 °C ( $\text{Time} = -208.0 + 19.70 \text{ Total length}$ ,  $\text{Distance} = -2.080 + 0.197 \text{ Total length}$ ) ( $n = 8$  to  $12$  individuals per time period).

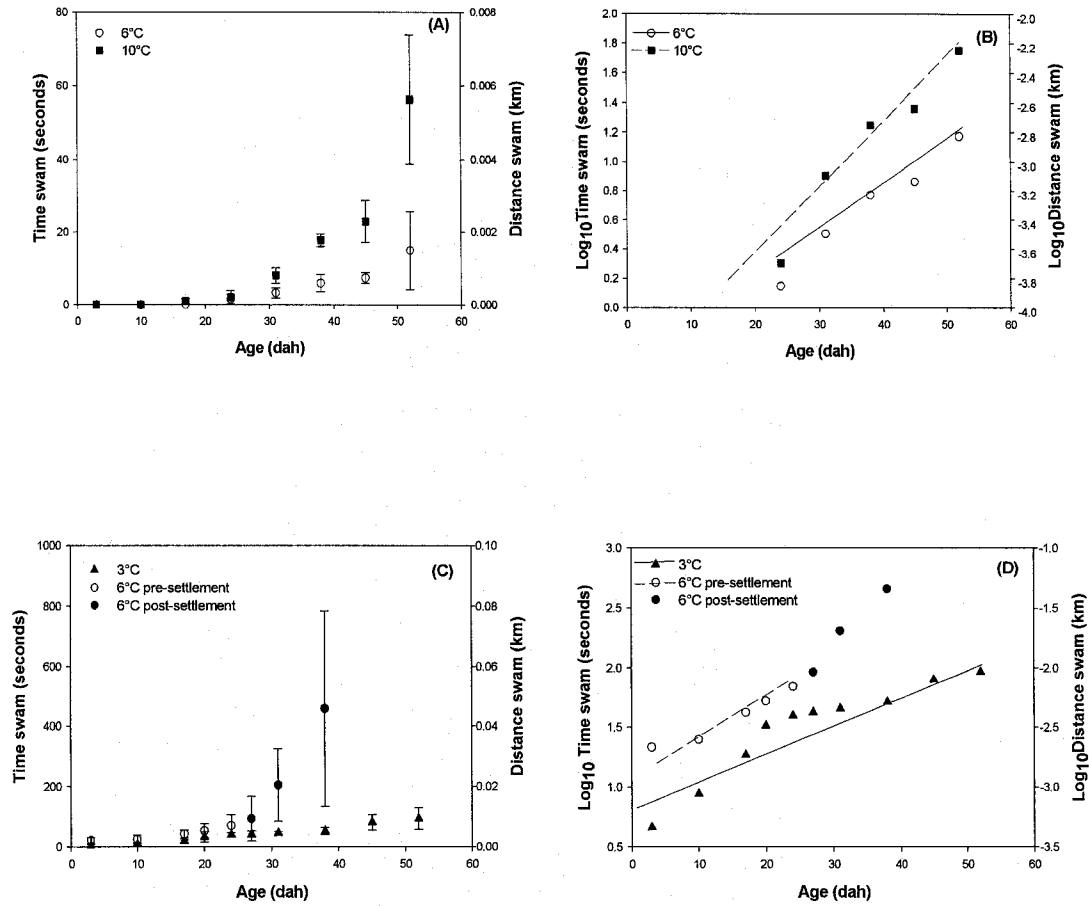


Figure 3.2. Development of sustained swimming time (seconds) and swimming distance (km) with absolute age (days after hatch) for different rearing temperatures. (A) Non-transformed values for cod larvae at 10 °C and 6 °C, (B) Log<sub>10</sub>-transformed cod larvae at 10 °C ( $\text{Log}_{10} \text{Time} = -0.840 + 0.051 \text{ dah}$ ,  $\text{Log}_{10} \text{Distance} = -5.150 + 0.0581 \text{ dah}$ ) and 6 °C ( $\text{Log}_{10} \text{Time} = -0.279 + 0.0258 \text{ dah}$ ,  $\text{Log}_{10} \text{Distance} = -4.620 + 0.0345 \text{ dah}$ ), (C) Non-transformed values for sculpin larvae at 6 °C pre-settlement, 6 °C post-settlement and 3 °C, (D) Log<sub>10</sub>-transformed for sculpin larvae at 6 °C pre-settlement ( $\text{Log}_{10} \text{Time} = 1.210 + 0.0254 \text{ dah}$ ,  $\text{Log}_{10} \text{Distance} = -0.792 + 0.0254 \text{ dah}$ ), 6 °C post-settlement and 3 °C ( $\text{Log}_{10} \text{Time} = 0.809 + 0.0253 \text{ dah}$ ,  $\text{Log}_{10} \text{Distance} = -1.190 + 0.0253 \text{ dah}$ ) ( $n = 8$  to  $12$  individuals per time period).

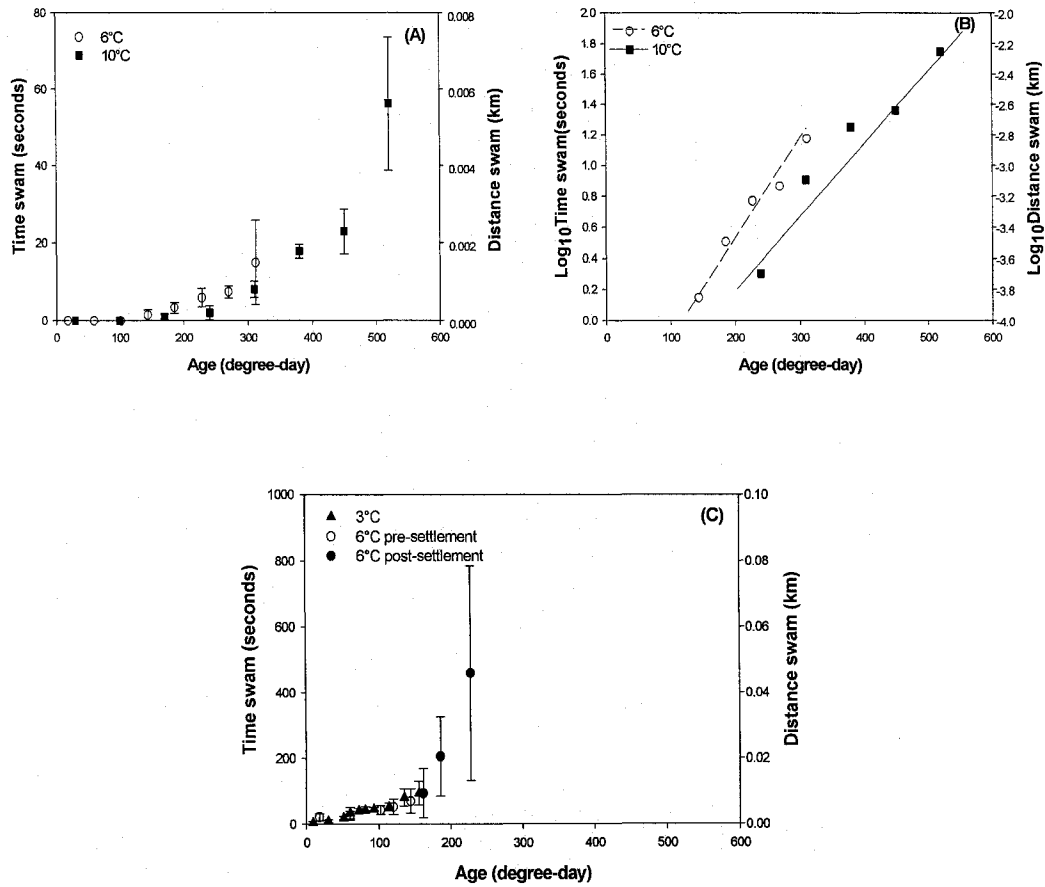


Figure 3.3. Development of sustained swimming time (seconds) and swimming distance (km) with thermal summation age (degree-days) under different rearing temperatures. (A) Non-transformed values for cod larvae at 10 °C and 6 °C, (B) Log<sub>10</sub>-transformed cod larvae at 10 °C ( $\text{Log}_{10} \text{Time} = -0.840 + 0.0051 \text{ degree-days}$ ,  $\text{Log}_{10} \text{Distance} = -5.150 + 0.0058 \text{ degree-days}$ ), 6 °C ( $\text{Log}_{10} \text{Time} = -0.618 + 0.0057 \text{ degree-days}$ ,  $\text{Log}_{10} \text{Distance} = -4.620 + 0.0057 \text{ degree-days}$ ), (C) Non-transformed values for sculpin larvae. 6 °C pre-settlement, 6 °C post-settlement and 3 °C ( $\text{Time} = -7.060 + 0.6080 \text{ degree-days}$ ,  $\text{Distance} = -0.071 + 0.0060 \text{ degree-days}$ ) ( $n = 8$  to 12 individuals per time period).

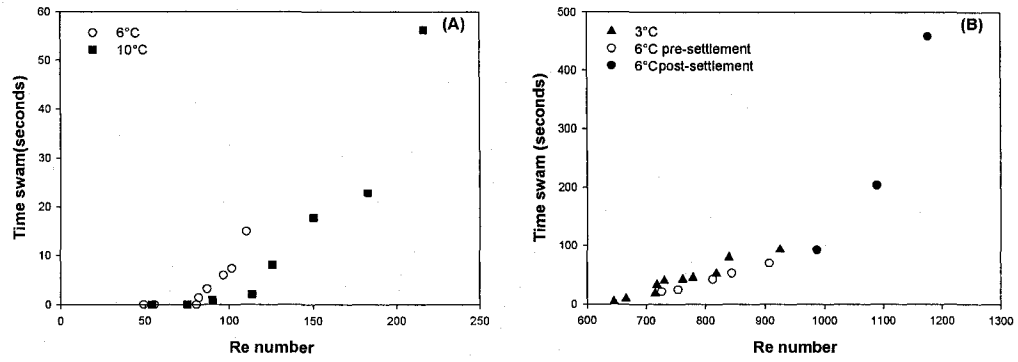


Figure 3.4. Development of sustained swimming ability with Reynolds ( $Re$ ) numbers under different rearing temperatures. (A) Sustained swimming ability with  $Re$  for cod larvae, (B) Sustained swimming time with  $Re$  for sculpin larvae ( $n = 8$  to 12 individuals per time period).

## **Chapter 4 - Implications for larval dispersal in strongly seasonal environments: Transport of larvae from pelagic and demersal spawners in Placentia Bay, Newfoundland**

### **4.1 Introduction**

For many species, it is thought that dispersal takes place primarily during the pelagic larval stage (Leis and Carson-Ewart, 1997; Leis, 2006), and the success and failure of larval recruitment is a major determinant of population structure and dynamics (Stobutzki and Bellwood, 1994). In the last decade, there has been a widening belief that the pelagic stages of larval fish are capable of actively modifying their dispersal (e.g. Cowen *et al.*, 2000; Leis, 2006), and a coincident increase in interest in early life history stages and factors that influence recruitment variation (Blaxter, 1974; Sherman, 1984). Green and Fisher (2004) noted that replenishment of adult populations of many marine fishes occurs through a pelagic larval phase and fish larvae can potentially modify their patterns of dispersal during this phase using active swimming behaviour. Larvae can have greater control over their position and trajectory if they are effective swimmers (Stobutzki and Leis, 1999) and some individuals can swim faster than average ambient current speeds (Leis *et al.*, 2000; Leis, 2006). To fully understand the potential importance of active swimming capabilities of larvae in modifying their dispersal, there is a need for studies that consider the roles of both physical oceanography and the active behavioural contribution of larval fish.

Miller et al. (1988) indicated that prior to settlement larvae of many species are capable of swimming against currents and can potentially cover considerable distances (Stobutzki and Bellwood, 1994; Leis, 2006). Because swimming and active habitat selection can contribute significantly to dispersal (reviewed by Bradbury and Snelgrove, 2001), good swimming performance is often a necessary component of self-recruitment (Leis and Carson-Ewart, 2000). Lab studies on critical ( $U_{crit}$ , maximum speeds maintained for 2 minutes, Chapter 2) and sustained swimming capabilities of cold-water larval fishes (Chapter 3) suggest that larvae in coastal Newfoundland have some capacity to influence their arrival at a suitable settlement location.

Physical mechanisms also can affect multiple biological factors such as reproductive location, larval transport, and movement leading to settlement. The mechanisms that disperse and concentrate fish larvae include large and small-scale influences on spatial and temporal distribution patterns. In complex ocean environment, large-scale and regional currents, eddies, Taylor columns, wind forcing, tidal currents, oceanographic gyres, frontal zones, and hydrothermal plumes all can contribute to larval transport and dispersal (Bradbury and Snelgrove, 2001). Attempts to explain the observed horizontal distributions of larvae have often required invoking interplay between the active behaviour of larvae and the physical environment (e.g. Werner *et al.*, 1993), and



biological oceanographic modellers are now beginning to incorporate active larval swimming behaviours into dispersal models (e.g. Cowen, 2002; Cowen *et al.*, 2006) with particular recognition of the importance of active behaviour in coral reef species. The interaction of physical mechanisms (see Bradbury *et al.*, 2003) and active larval transport processes that integrate ecology, physiology, and behaviour variables with physical oceanography (Sponaugle *et al.*, 2005) provide an emerging tool to predict larval trajectories under realistic flow conditions that has important conservation and management applications (Paris and Cowen, 2004). For example, simple models can demonstrate the sensitivity of a given process under particular conditions, whereas more sophisticated models will be able to help predict where, when, and how many larvae are likely to recruit to a given region (Warner and Cowen, 2002). Studies that combine laboratory studies on swimming capabilities of fish larvae with field studies on physical transport in seasonal environments may lead to better predictions of larval fish dynamics under realistic environmental conditions (Bradbury and Snelgrove, 2001), and ultimately to improve our capacity to predict recruitment and spatial patterns in fish populations.

In order to evaluate the role that active swimming behaviour may play in the dispersal of larval fish in cold water environments, I placed the experimental findings on critical and sustained swimming speeds from the previous chapters in the context of field data. I applied data on swimming capability to simulations of fish larval transport in

Placentia Bay, Newfoundland, to determine whether observed field distribution patterns corresponded to predictions based on simple modeling. Specifically, I ask, are simple models of passive larval dispersal in two fish species with contrasting life-history strategies adequate to explain observed field distribution patterns in a representative coastal embayment, or are patterns more consistent with simulations of active larval dispersal that combine active locomotion behaviour, temperature-dependent development, and physical transport mechanisms?

## **4.2 Materials and Methods**

### *Area Selection*

Placentia Bay (Fig. 4.1) is a large embayment on the south coast of Newfoundland measuring 130 km in length and 100 km in width. Circulation data (Schillinger *et al.*, 2000) indicate strong and relatively consistent flow into the bay along the eastern side, weak and variable flow at the head, and south-westerly flow out of the western side of the bay (Bradbury *et al.*, 2000; Snelgrove *et al.*, accepted). Recent work on larvae of cod (Bradbury *et al.*, 2000) and other species (Snelgrove *et al.*, accepted) provides evidence for potential offshore flushing of larvae from the bay as a result of the predominant circulation. Physical conditions in the bay show strongly seasonal change in water properties; water temperatures in the spring and summer vary from 0-2 °C in April to 10 °C in June to ~15 °C in August (Snelgrove *et al.*, accepted).

### *Model definition and simulation approach*

Larval drift routes are commonly simulated by utilizing a Lagrangian particle tracking technique, but I lacked detailed spatial data on circulation necessary to generate an accurate and detailed circulation field. I therefore simulated larval transport by including both physical transport, in the form of mean currents, and biological contributions in the form of data on critical swimming speed, sustained swimming ability, and pelagic larval duration. In order to estimate physical transport, Placentia Bay was divided into 4 regions based on the positions of 6 mooring sites (Fig. 4.1). At the head of the bay, the mean current data at moorings 5 and 6 provided an estimate of mean flow in the western and eastern sides near the head of the bay. Similarly, mean current data at moorings 1 and 2 were averaged to provide an estimate of flow speed and direction near the mouth of the western side of the bay mouth and moorings 3 and 4 were averaged to provide mean flow speed and direction estimates near the mouth of the eastern side of the bay.

Generally, fish larvae can use critical swimming capacity for high-speed, short-term movement such as escape responses or vertical migration. Pre-flexion larvae are located predominantly in the upper 40 m of the water column (Pepin *et al.*, 1997), with most individuals near the surface (0-20 m). In coastal Newfoundland waters, post-flexion larvae are often distributed within deeper layers. For passive transport simulations, I assumed that fish larvae stay near the surface and do not vertically

migrate during transport. Therefore, the transport trajectory was based entirely on current speeds within the surface layer (0-30 m), which was estimated from mean currents measured at 20 m. For simulations that included an active behavioural component (hereafter active transport), I divided the water column into a surface layer (0-30 m) and deeper layer (>30 m) using the available current meter data from 20 m and 45 m respectively, and assumed that fish larvae moved unidirectionally from the surface layer to the deeper layer during development. My observations on behaviour and morphology of late larval-early juvenile cod and settlement-age sculpin suggest that cod shift to greater depths around 15-20 dah, whereas sculpin shift to the deeper layer during the early post-flexion stage at ~17-24 dah depending on water temperature.

Work in Placentia Bay during 1997-1999 (Lawson and Rose, 2000; Bradbury *et al.*, 1999, 2000) indicated two major spawning sites for cod at Bar Haven and Oderin Bank (Fig. 4.1), both situated on the western side of the bay. Information from the same survey suggested that a major spawning site for sculpin was near Placentia, on the eastern side of the bay near the shoreline. These sites were therefore chosen as starting positions for larval transport simulations. Larvae were then moved from these starting points by passive transport (mean current only) or active transport (combination of mean current and active swimming speeds), where composite swim speed in active transport is defined as:

Composite swim speed ( $VM_t$ ) = Mean current speed ( $VM_c$ ) + 0.5 \* Larvae swimming speed ( $VM_f$ ),

where larval swim speed is set at 50% of critical swim speed and swim direction was varied depending on adjacent shoreline geography (see below).

Larvae were then moved through the bay in weekly steps using only the mean current speed in the passive transport scenario and at the composite speed for the active transport scenario. The transport distance and new position for the passive transport simulation was calculated as:

Potential total travel distance ( $D_p$ ) = Current speed \* Passive transport time

The transport distance and new position for the active transport simulation was calculated as:

Potential total travel distance ( $D_a$ ) = Composite speed \* Active swimming time +  
Current speed \* Passive transport time,

where a portion of the total travel distance was assumed to be passive and a portion of the distance was assumed to be partly active (see below).

In both simulations, the new position was calculated as:

New position ( $L_p(T+1)$ ) = (Old position ( $L_p(T)$ ) + Travel Distance ( $D$ )) / 111.7011

Timing of spawning and hatch also differed for the two species (Snelgrove *et al.*, accepted). Because sculpin hatch in spring, water temperatures of 3 and 6 °C were used in separate simulations of early and late spring. Atlantic cod in Newfoundland

usually spawn in spring as early as March in the northern part of its range and spawning may then continue into late summer (e.g. Lawson and Rose, 2000). Temperatures of 6 and 10 °C were therefore used in separate simulations of late spring and summer conditions.

Studies of multiple reef fish species suggest that 50%  $U_{crit}$  provides a reasonable estimate of sustainable swimming speed across large distances (Clark. *et al.*, 2005), and can be used to estimate sustainable speed for theoretical larval dispersal models (Fisher and Wilson, 2004). In the absence of comparable data for cold-water species, I therefore used 50% of  $U_{crit}$  values determined from my laboratory measurements on cod and sculpin (Chapter 2) as an optimistic estimate of sustainable larval swim speeds in the simulations. Studies of multiple reef fish species also suggested 12 hours was a reasonable time for larvae to maintain sustained swimming on a daily (24 hour) basis, and this time was therefore used to estimate active sustained swim time in the active transport simulation. Given the poorer swimming performance of these cold-water species relative to reef species (Chapters 2, 3) this value is almost certainly an overestimate of swim time. Reef fish have also been shown to orient themselves relative to potential reef settlement sites (Leis *et al.*, 1996, 2003). In my simulations, I assumed that larvae would orient themselves towards the shoreline where appropriate juvenile habitat is found (see Bradbury *et al.*, 1999; Snelgrove *et al.*, accepted) and that they would try to avoid transport to offshore areas where higher mortality would

be anticipated.

The choice of swim direction was complicated by the different release points for larvae of the two species relative to the geography of the bay and by differences in swimming ability at hatch (Chapter 2). For sculpin, larvae were assumed to hatch on the eastern side of the bay, so that swimming to the east would allow them to locate nearshore habitat where they could potentially remain until settlement. Swimming directly south would move them away from the coast, which was undesirable. I therefore assumed potential swimming directions of 70, 90 or 135 °TN (°TN denotes true north) in simulations. For cod, which are much weaker swimmers that were assumed to hatch on the western side of the bay, I used swimming directions of 0, 225, 270 and 315 °TN in separate simulations; all of these directions would move larvae towards the nearby shoreline. Additional simulations were also run with directions of 25, 45, 90, 135, 180 and 335 °TN. All of these directions were possible because larvae were sufficiently weak swimmers that they would not move outside the simulation area (and into shoreline habitat) no matter which direction they were allowed to swim. I then compared the simulated passive (no swimming) and active transport trajectories to field distribution patterns of larvae in Placentia Bay in order to determine whether model predictions were consistent with field patterns either with or without swimming behaviour. Specifically, were spatial patterns in larval size distributions consistent with passive or active predictions, assuming that larger individuals in field surveys

were spatially representative of where smaller individuals would be transported over time?

Finally, in order to allow a more direct comparison of active swimming behaviour of sculpin and cod, and to compare the effect of spawning locations on dispersal or retention, I conducted simulations where sculpin larvae were initiated from the same initial locations as cod larvae. Thus, if larvae from pelagic and bottom spawners were released from the same locations, would there be differences in their capacity to remain within the bay? If sculpin larvae were hatched on the west coast in the same area as cod larvae, would they have similar potential for dispersal or retention? This comparison was not intended to simulate field patterns but instead to provide a direct comparison between the two species and the different spawning locations.

#### Field Data

Ichthyoplankton distribution patterns were determined from samples collected at each of 45 stations (Fig. 1) using a 2 m x 2 m Tucker trawl with decreasing mesh sizes of 1000, 570, and 333  $\mu\text{m}$ . Flow volumes were estimated from two General Oceanic flowmeters placed at the mouth of the net, which sampled obliquely to a maximum depth of 40 m for 15 min. duration at a towing speed of  $\sim 2$  knots. This depth range has been shown to encompass  $> 95\%$  of the ichthyoplankton in coastal Newfoundland (Frank and Leggett 1982; Laprise and Pepin 1995).

#### 4.3 Results



***Gadus morhua* (Atlantic cod):**

*Passive transport simulation*

For eggs hatched at Bar Haven (Fig. 4.1) near the head of the bay, cod larvae in the simulation were flushed by southwesterly currents past Oderin Bank in the first week and out of the mouth of the bay in the second week (Fig. 4.2 A). For the second larval release location (Oderin Bank, 47.247 °N, 54.703 °W) on the western side of Placentia Bay, the passive transport simulation indicated that cod larvae would be flushed from the bay within 1 week after hatch (Fig. 4.3 A).

*Active transport simulation*

For larvae hatched at Bar Haven (Fig. 4.2 B) at the head of the bay, if larvae hatched early in late May or early June when water temperatures are 6 °C or less, my laboratory observations suggest that it would take ~24 days for cod larvae to develop to an early post-flexion stage where they would begin to display vertical migration. During the first week after hatch at this temperature, larval mean swimming speed was  $1.17 \text{ cm} \cdot \text{s}^{-1}$ , which is much slower than mean current speeds. For this simulation, irrespective of swimming direction, larvae were transported south along the western side of the bay past Oderin Bank during the first week of development. By the second week after hatch, cod larvae were predicted to be flushed from the bay (Fig. 4.2 B). Given their predicted size and my behavioral observations, larvae would not have been expected to move vertically into the deeper layer prior to flushing.

If eggs were hatched later in late August or early September when mixed layer average water temperatures would be  $\sim 10^{\circ}\text{C}$ , the critical swimming speed would be  $\sim 1.93\text{ cm}\cdot\text{s}^{-1}$ , which is still much slower than mean current speeds. Both the speed and size would be significantly greater than cod larvae developing at  $6^{\circ}\text{C}$  for a given absolute age (Chapter 2). At these temperatures, it would take only  $\sim 17$  days for larvae to develop to the early post-flexion stage and move to the deeper layer. For this simulation, irrespective of swimming direction, larvae were also transported south past Oderin Bank during the first weeks, then were flushed from the bay during the second week prior to moving into the deeper layer (Fig. 4.2 C).

For the second egg release position at Oderin Bank on the western side of Placentia Bay, flushing times were even faster. For this simulation, irrespective of swimming direction, cod larvae were flushed from the bay area by the strong southwesterly currents within the first week after hatch (Fig. 4.3 B). If eggs were hatched later in late August or early September when mixed layer temperatures would be  $\sim 10^{\circ}\text{C}$ , then critical swimming ability would be significantly faster and size would be significantly greater for a given absolute age, however, cod larvae were again flushed from the bay within the first week after hatch irrespective of swimming direction (Fig. 4.3 C).

***Myoxocephalus scorpius* (Shorthorn sculpin):**

### *Passive transport simulation*

I assumed that for the first 1-2 weeks after hatch at Placentia, sculpin larvae were transported north along the eastern side of Placentia Bay with the mean current toward the head of the bay. In the subsequent weeks, larvae were transported by the southwestern current along the western side of the bay (Fig. 4.4. A) before being flushed out of the bay during the 6<sup>th</sup> week. For the warmer temperatures, because settlement is predicted to occur in 5 weeks after hatch, it is possible that larvae could settle to the bottom prior to being flushed from the bay, even in a scenario of passive transport.

### *Active transport simulation*

If larvae hatched at Placentia in early April when water temperatures are 3 °C or less, my laboratory observations suggest that it would take ~24 days for sculpin larvae to develop to an early post-flexion stage where they would begin to display vertical migration. During the first week after hatch at this temperature, larval mean swimming speed was  $6.46 \text{ cm}\cdot\text{s}^{-1}$ , which is within the same range as mean current transport speeds (mean  $10.96 \text{ cm}\cdot\text{s}^{-1}$  along a north-south (u) axis and  $8.48 \text{ cm}\cdot\text{s}^{-1}$  in the east-west axis (v)), but the swim speed used for the simulation was only  $3.23 \text{ cm}\cdot\text{s}^{-1}$ . For this simulation I found that for 70-135 °TN swim trajectories during the first 1 to 2 weeks, larvae were moved north along the eastern side of Placentia Bay (Fig. 4.4.B), with larval active swimming ability increasing gradually and individuals moving into

the deeper layer after 24 days (Chapter 2). As in the passive transport simulation, sculpin larvae in this simulation remained along the eastern side of bay for the first 2 weeks, however, once at the head of the bay, larvae were of a sufficient size and swimming ability that the only swimming direction that did not result in retention within the bay was to swim with the current, which would flush the larvae from the bay and would only be expected if larvae were attempting to move offshore. These results suggest that active swimming could play a major role in larval retention after the 2-3 weeks. At 3 °C, the swimming direction had no substantial effect on simulation results for the first 1-2 weeks.

When larvae were hatched at the same place later in April or early May when surface water temperatures in coastal Newfoundland could reach 6 °C, my laboratory experiments indicate that critical swimming ability of larval sculpin would be significantly faster and size would be significantly greater for a given absolute age than would be expected for larvae hatched in early April. At the warmer temperatures, it would take only ~17 days for larvae to develop to the early post-flexion stage and move to the deeper layer. For this simulation, larvae also moved north along the eastern side (Fig. 4.4.C). After hatching near Placentia, if I assume larvae swim directly towards the shoreline (90 °TN), they would be retained near the eastern coast until settlement. If I assume larvae swim opposite to the current (135 °TN), they would still be transported north along the east coast for the first 2 weeks, but their

swimming ability would be such that they could then swim towards the south in subsequent weeks until settlement on the eastern side of the bay. If I assume that larvae swim approximately with the current along the eastern side ( $\sim 70^\circ \text{TN}$ ), then they would arrive at the head of the bay in the third to fourth week of development. Given that the time from hatch to settlement at this temperature is predicted to be  $\sim 5$  weeks (Chapter 2), larvae would then be expected to remain at the head of the bay or travel along the western side of the bay until they were sufficiently developed to settle into coastal bottom habitat. This result is consistent for any trajectory except for swimming with the current, which would again carry them offshore. Compared to the passive transport simulation, sculpin larvae in this simulation remained within the bay, indicating that active swimming of sculpin larvae can significantly contribute to larval dispersal.

To compare sculpin larval dispersal directly to that of cod larvae and to examine the role of spawning location, I simulated release of newly hatched sculpin larvae from Bar Haven and Oderin Bank (the cod larvae hatch sites). If released from Bar Haven, irrespective of temperature, during the first week of development sculpin larvae would travel with the southwestern current along the western side of the bay where they would be flushed past Oderin Bank and out of the bay by the second week (Fig. 4.5 A and B). Temperature had no effect on simulation results, whereas active swimming direction had a substantial effect on dispersal trajectories but limited effect on the

outcome. Not surprisingly, sculpin larvae released from Oderin Bank would also be flushed from the bay before developing to a large enough size to overcome surface currents, irrespective of temperature.

#### *Field Observations*

In the June survey, the smallest cod larvae (~ 2.0-4.0 mm) were distributed near Bar Haven and south of Oderin Bank (Fig. 4.6 C). The passive and active transport simulations yielded similar results at 6 °C; cod larvae hatched at Bar Haven would be expected to appear north of Oderin Bank at a size of ~5.0-7.0 mm, whereas larvae of this size that were hatched at Oderin Bank would be expected to occur further south on the outer western side of the bay. This pattern is consistent with field observations (Fig. 4.6.C). Based on the simulations, larvae were expected to be flushed from the bay from either release point before reaching a size of 7.0 mm, however, some larvae of this size were observed in field samples south of Oderin Bank and near Bar Haven, suggesting greater retention than the simplified simulation would predict.

In the August survey, cod larvae of ~2.0-4.0 mm were observed primarily along the west side of the bay south of Oderin Bank, but some individuals were also collected near the head of the bay (Fig. 4.6D). The passive and active transport simulations yielded similar results at 10 °C. In these simulations, larvae of ~5.0-7.0 mm were expected to occur from south of Oderin Bank to the mouth of the bay, which was

generally consistent with field observations. Nonetheless, there were also some individuals of this size on the eastern side of the bay, which may have been related to a third spawning aggregation known to occur near the southeastern most point of the bay (Lawson and Rose, 2000). Older larvae of ~8.0-13.0 mm were expected to be flushed from the bay; however, some individuals of this size were concentrated near Oderin Bank and on the eastern coast. Again, this pattern suggests greater larval retention than the simple simulation would suggest.

In April when the water temperature is ~3 °C, the smallest sculpin larvae in field surveys were ~6.0-11.0 mm, and were found along the east side of the bay north of Placentia (Fig. 4.6 A). In the sculpin simulation, larvae were assumed to hatch at ~10.5-11.0 mm near Placentia, which corresponds to the high end of the range of sizes in spring field surveys but was consistent with data on hatching of laboratory-reared individuals at this temperature (Chapter 2). The active transport simulations indicated that larvae would be concentrated on the east side of the bay, whereas the passive transport simulations indicated that larger larvae would be concentrated on the western side of the bay. Larvae in active simulations were transported northward along the east coast of Placentia Bay, where larvae of ~11.0-12.0 mm were predicted to occur. Active simulations were consistent with field observations of high concentrations of larvae of that size. Nonetheless, some larvae of this size also appeared at the centre of the bay. Laboratory-reared larvae grew to ~17.0-18.0 mm after ~ two months (Chapter 2), and

in the passive transport simulation, larvae of this size would be expected to be flushed from the western side, which is in contrast to patterns observed in field data. Specifically, there were individuals of this size and larger at the head of the bay and in the centre of the bay (Fig. 4.6 B), which is also consistent with active simulations in which the larger larvae are sufficiently well developed that they can move anywhere within the bay.

#### **4.4 Discussion**

Many physical oceanographic mechanisms can affect spawning location, larval transport and settlement processes. Realistic attempts to explain spatial patterns in larvae must consider the interplay between larval active behaviour and physical transport mechanisms (Warner and Cowen, 2002). The passive and active simulations predicted larval transport routes in Placentia Bay where the velocity field was simplified to a counter-clockwise current pattern with fixed mean flows in different areas of the bay. These simple simulations suggest that active swimming performance and transport by currents both play significant roles in larval dispersal. However, the relative contributions of these variables to dispersal differ in these bottom and pelagic spawners as a result of the contrast in active swimming ability during the early pelagic phase. Temperature also plays an important role in the dispersal of bottom-spawning sculpin because it influences developmental stages through which substantial improvements in swimming ability occur. This effect is less obvious in



pelagic-spawning cod, where early larval stages are weak swimmers irrespective of rearing temperature.

Survey data from Placentia Bay showed that comparatively large numbers of cod eggs hatched at Bar Haven and Oderin Bank and, in some years, at the southeast most point of the bay (Bradbury *et al.*, 1999). In complex ocean environments, the weak swimming ability of early stage fish larvae would suggest that the rate and direction of larval advection depends primarily on near-surface currents (Bradbury *et al.*, 2001) and less on active control. In simulations with cod larvae, individuals hatched at Bar Haven traveled southward along the western side of the bay for 1 week before they were flushed from the bay; larvae that hatched at Oderin Bank were flushed out of the bay area in an even shorter time. Bradbury *et al.* (1999) observed a similar pattern in field surveys, and noted that larvae were concentrated near the exit boundary of the bay. The passive larval transport simulations, active larval transport simulations, and field observations on distributions considered in tandem suggest that the weak-swimming ability of cod larvae means that physical transport mechanisms dominate in environments like Placentia Bay where currents are relatively strong. During early development in particular, cod larvae are probably largely passive. The temperature effect on ontogenetic development is also relatively unimportant compared to the weak swimming ability of cod larvae in strong currents (Chapter 2). The simulation results also suggest that flushing of cod from the bay is quite likely,

particularly early in the summer. This finding increases the importance of knowing whether there is indeed increased mortality offshore, as suggested in other studies (Frank and Leggett 1982; Taggart and Leggett, 1987; Pepin *et al.* 1995).

Sculpin hatched on the east side of the bay, travelled northward to the head of the bay for the first few weeks after hatch, after which active swimming began to contribute significantly to potential dispersal. In the warmer (6 °C) temperature simulation, critical swimming speeds of sculpin larvae (see Chapter 2) had the potential to exceed mean surface currents from hatch onward, whereas the 50% critical swimming speeds used in the simulation were only greater than mean surface currents in individuals 1-2 weeks post hatch and onward, suggesting that larval active behaviour and physical transport both have the potential to influence dispersal after that developmental stage. Behaviour may be particularly important for bigger larvae with faster swimming speeds. In the colder temperature simulation, passive current transport was the major transport mechanism for the relatively smaller and slower larvae during the first 2-3 weeks after hatch. As Bradbury *et al.* (1999) suggested from field surveys, increases in water temperature can result in reduced larval dispersal and increase larval retention; my simple simulations of larval transport indicated a similar relationship between temperature and dispersal. In the warmer summer water, active swimming by larvae has a much greater potential to contribute to larval dispersal (and retention) than in the colder water conditions of early spring.

The simulation that compared cod and sculpin retention after releasing larvae from the same Bar Haven and Oderin Bank locations, though unrealistic relative to field spawning patterns, provides a direct comparison of dispersal potential between the pelagic and bottom spawners. This comparison illustrates that both species were flushed from the bay by the strong southwest current, although larvae from the bottom spawning sculpin had more of an influence on their dispersal trajectory than those of cod because of their superior swimming ability. This finding is consistent with the results from the previous chapters which showed that the sculpin larvae have stronger critical and sustained swimming abilities.

The simulation of cod and sculpin spawning at Bar Haven and Oderin Bank demonstrated that spawning location is also important for dispersal. When sculpin larvae hatched on the east coast and then were transported north along the east coast, they had time to grow to a sufficient size and swimming ability to actively control their swimming trajectories. However, sculpin larvae hatched on the west coast were quickly flushed from the bay, despite their comparatively larger size and stronger swimming ability. Thus, spawning location clearly plays a significant role in determining whether propagules are swept offshore or remain in the nearshore environment.

This dispersal simulation illustrates the potential interplay between behaviour and transport and is not intended to provide a realistic, predictive model. Indeed, it is limited from both a physical oceanographic and a biological perspective. From a physical perspective, the influences of wind, tides, nearshore topography and variability in surface currents were ignored. Wind is the major driving force in ocean circulation and is known to be a predominant influence on larval spatial pattern in coastal Newfoundland (Pepin *et al.*, 1995) and elsewhere (Voss *et al.*, 1999). In this simulation, wind was only considered in its contribution to mean currents while ignoring the important role of wind variation. Tidal flow, which can affect offshore and onshore transport, should also be considered. In the nearshore environment, currents interact with coastal features to create complex flows. All of these factors will potentially contribute to the transport and dispersal of fish larvae and should ultimately be included in more complex and realistic simulations. These additional sources of complexity may explain why field patterns indicate a greater degree of larval retention than the simulations would suggest. There are also limitations to the biological data. One complex issue is how to estimate swimming direction of fish larvae and associated behavioural cues. In coral reef species, the discrete nature of appropriate habitat (Leis *et al.*, 1996; Leis and Carson-Ewart, 1998) allows for a more clearly defined location for settlement compared to the more diffuse range of habitats that may be appropriate for the species considered in the present study. From an adaptive perspective, larvae in Newfoundland waters might be expected to move

towards areas of abundant food resources, or towards coastal areas where structural habitat is more readily available, but data to define larval endpoints for these species are few. It is also difficult to assign a single numerical value to swimming duration even for a defined size range of larvae, because this number may change over time periods of weeks. Moreover, active swimming ability increases gradually, rather than as a weekly step function as was used in this simulation. In short, the simulation presented here represents a preliminary first step in incorporating behavioural and physical components into a dispersal model.

It is often challenging to achieve consistency between field data and model predictions because of the difficulties in simulating realistically the flow environment in which larvae live (Mora and Sale, 2002). Roberts (1997) used simple models of long-term average surface currents in the Caribbean to predict a general larval distribution pattern which contradicted known spatial pattern of some species in this region. A study that compared observed field patterns of coral larvae near the Great Barrier Reef and predicted larval concentrations from a dispersal model also found no correlation between the empirical data and the model (Oliver *et al.*, 1992). In my simulations of larval dispersal in sculpin, the model simulations that considered active swimming behaviour generated dispersal patterns that were generally consistent with field observations. However, for pelagic-spawning cod, neither the active nor the passive transport simulation could explain the observed field spatial pattern, suggesting that

larval retention is more complex than these simulations predict. Models represent simplifications of many factors that affect the larval dispersal process and, as a result, simple model outputs cannot accurately predict field patterns (Mora, 2002). Thus, modelling is an important technique which can yield novel insights, but it is important to recognize limitations, as well as the shortage of biological information available to improve their predictive capability.

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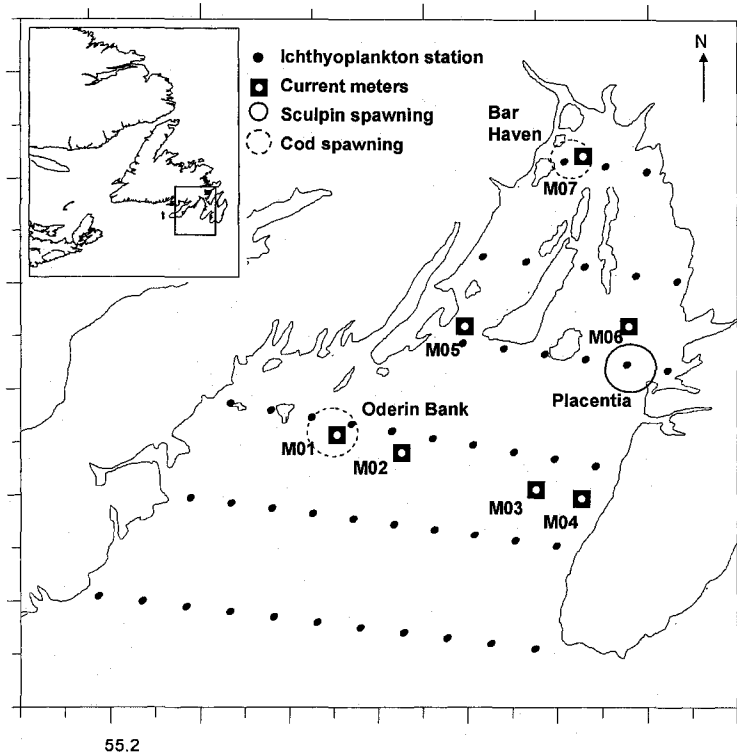


Figure 1 - Guan and Snelgrove, 2006

Figure 4.1. Map of Placentia Bay showing hatch sites of cod and sculpin larvae and mooring locations. Hatched circles represent major larval hatching sites for cod (Bar Haven, Oderin Bank) as inferred from field patterns in eggs and recently-hatched larvae whereas the solid circle indicates the major hatch site for sculpin (Placentia) as inferred from field patterns in small larvae. Squares and associated labels indicate mooring sites (Bradbury et al., 1999; Schillinger et al., 2000).

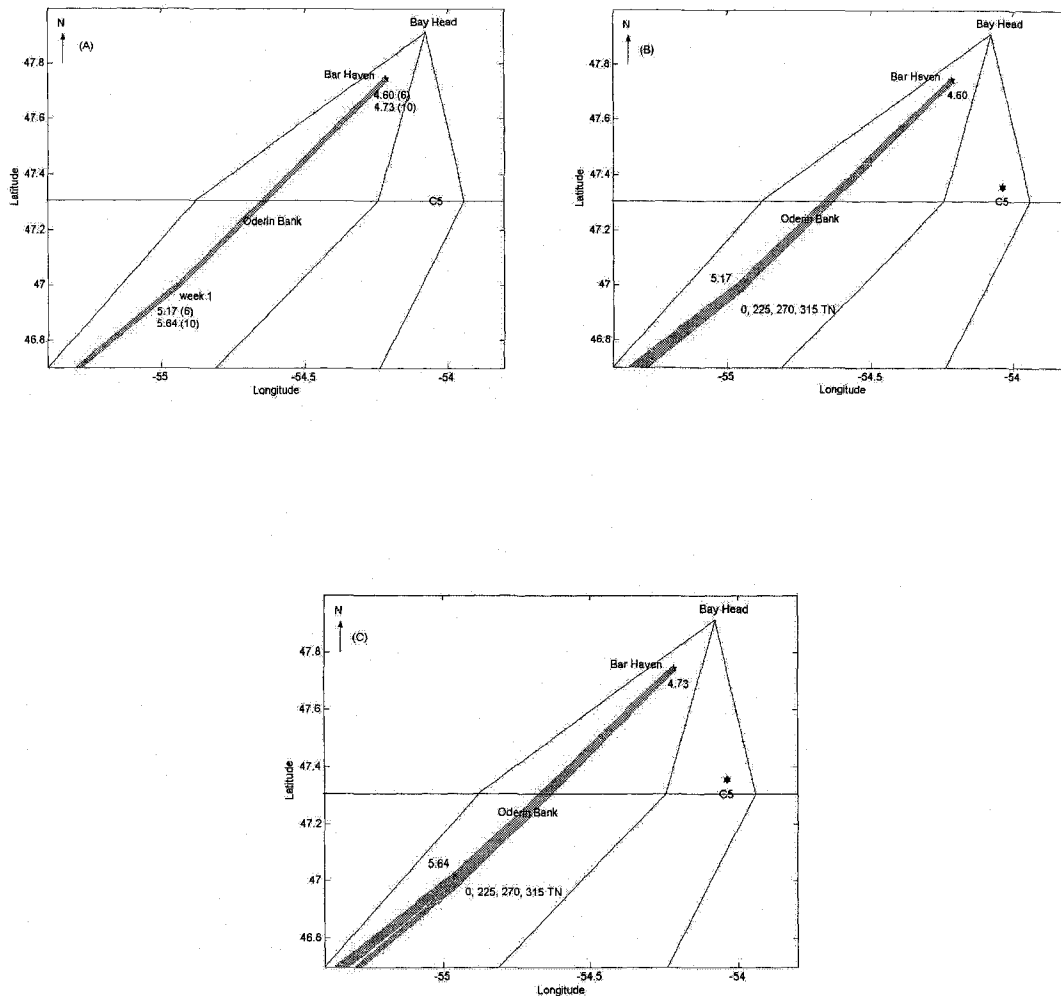


Figure 4.2. Simulated Atlantic cod larvae transport in Placentia Bay, for larvae initially hatched at Bar Haven. (A) Passive transport simulation (temperature in parentheses). (B) Active transport simulation, 6 °C (0, 225, 270 and 315 °TN). (C) Active transport simulation, 10 °C (0, 225, 270 and 315 °TN), where TN denotes True North. Numbers next to transport trajectories indicate predicted larval size in mm. Green line indicates larval transport route.

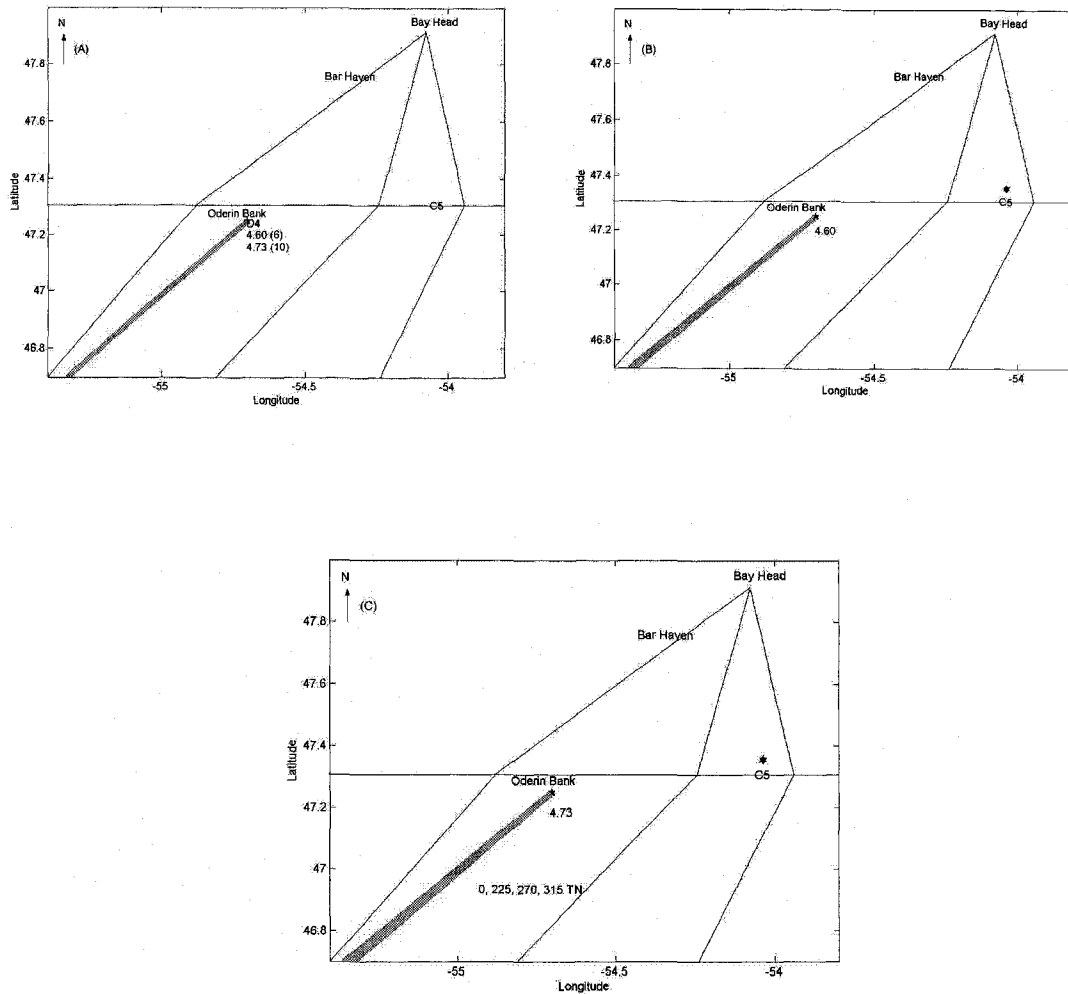


Figure 4.3. Simulated Atlantic cod larvae transport in Placentia Bay, for larvae initially hatched at Oderin Bank. (A) Passive transport simulation (temperature in parentheses), (B) Active transport simulation, 6 °C. (0, 225, 270 and 315 °TN), (C) Active transport simulation, 10 °C. (0, 225, 270 and 315 °TN), where TN denotes True North. Numbers next to transport trajectories indicate predicted larval size in mm. Green line indicates larval transport route.

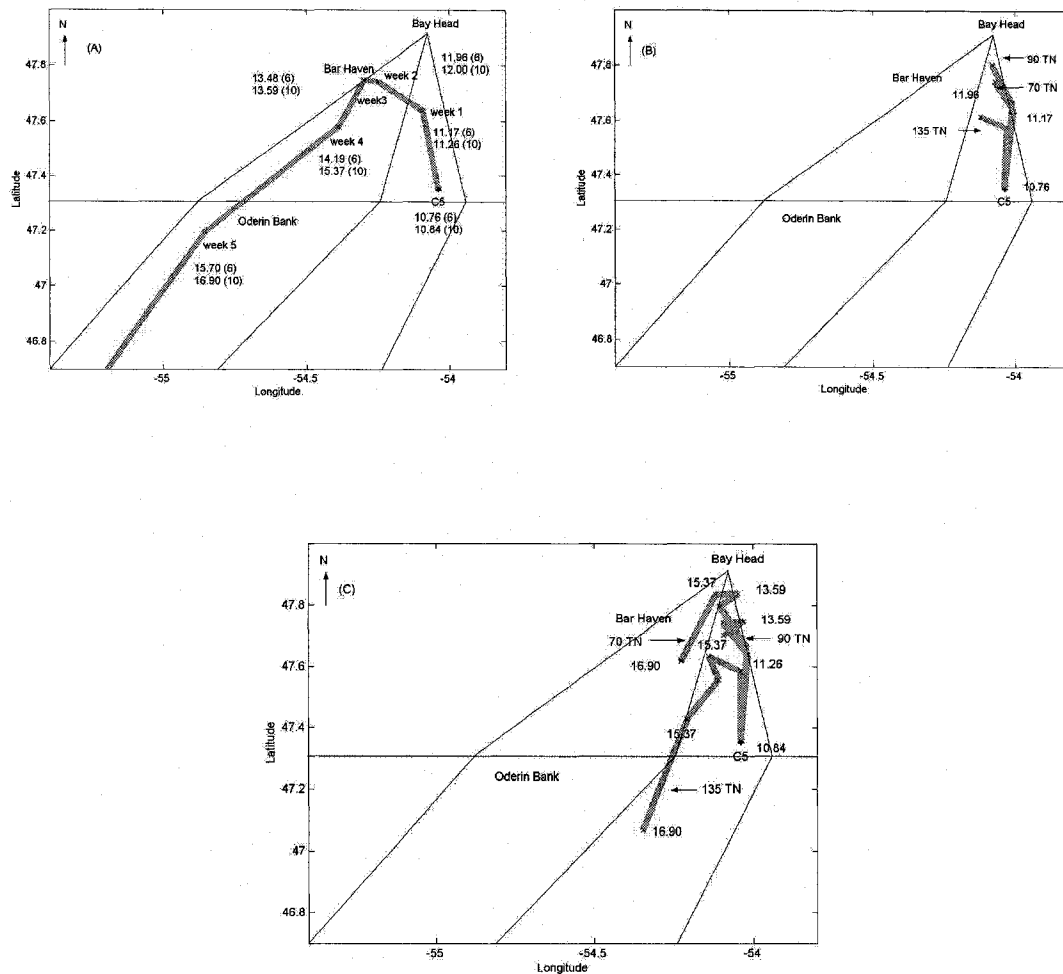


Figure 4.4. Simulated shorthorn sculpin larval transport in Placentia Bay for larvae initially hatched near Placentia. Numbers next to transport trajectories indicate predicted larval size in mm. (A) Passive transport simulation (temperature in parentheses), (B) Active transport simulation, 3 °C (70, 90 and 135 TN), (C) Active transport simulation, 6 °C (70, 90 and 135 TN), where TN denotes True North. Numbers next to transport trajectories indicate predicted larval size in mm. Green line indicates larval transport route.

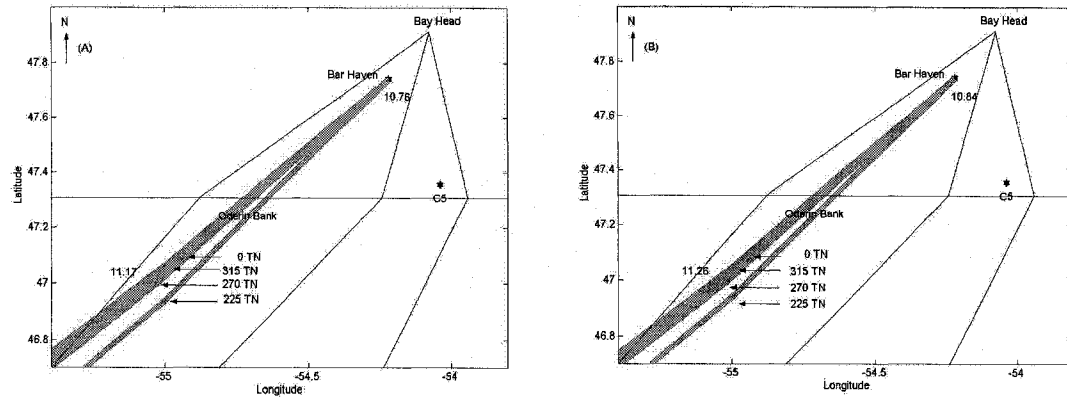


Figure 4.5. Simulated shorthorn sculpin larval transport in western Placentia Bay, for larvae initially hatched at Bar Haven. Numbers next to transport trajectories indicate predicted larval size in mm. (A) Released at Bar Haven, 3 °C (0, 225, 270 and 315 TN), (B) Released at Bar Haven, 6 °C (0, 225, 270 and 315 TN), where TN denotes True North. Numbers next to transport trajectories indicate predicted larval size in mm. Green line indicates larval transport route.



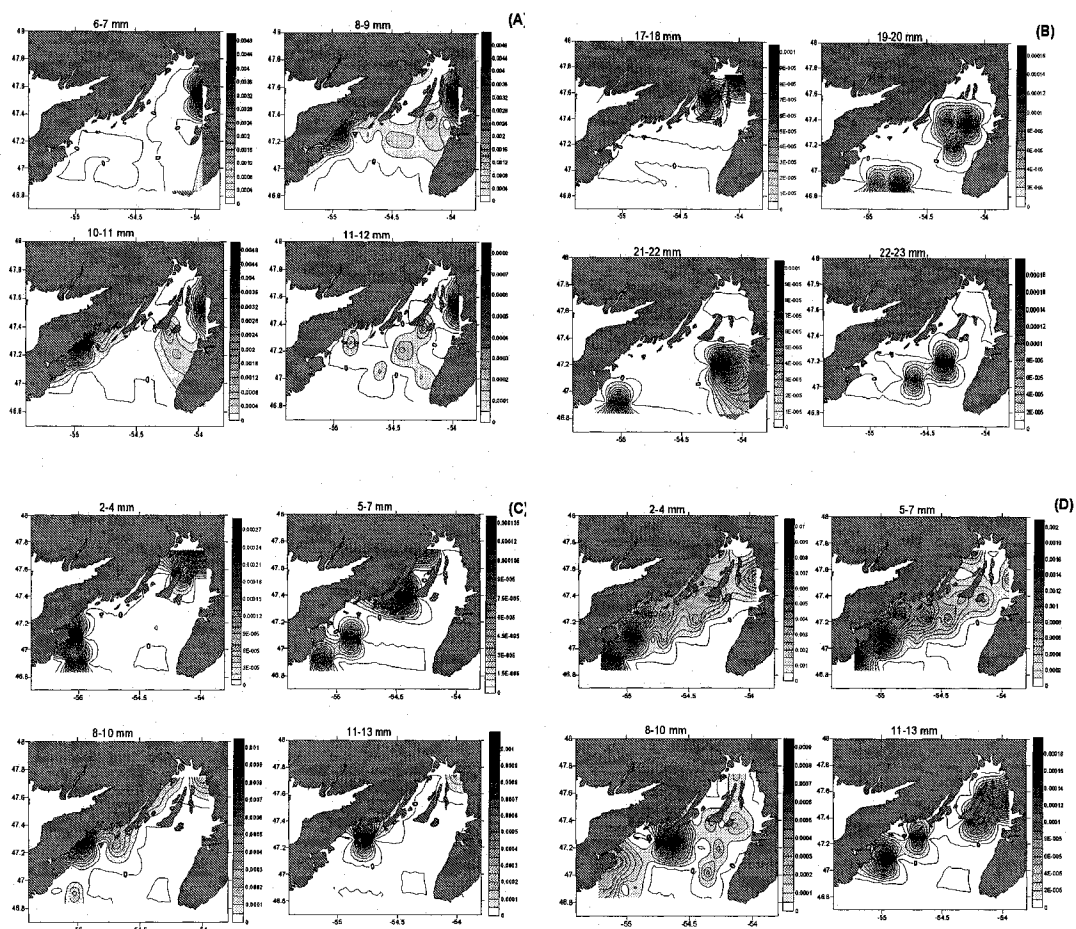


Figure 4.6. Average distribution of larvae of (A) Shorthorn sculpin in April, (B) Shorthorn sculpin in June, (C) Atlantic cod in June and (D) Atlantic cod in August. Scale indicates # per 1000 m<sup>3</sup> sampled at 45 stations in Placentia Bay from 1997-1999.

## Summary and Conclusions

The introductory chapter examines the possible importance of larval fish active swimming behavior in determining spatial and temporal patterns, population dynamics, and recruitment variation in marine ecosystems. This summary also suggests that size is a primary factor in predicting swimming ability of fish larvae; however, environmental temperature also can affect their swimming ability in the pelagic larval stage by influencing development rate of swimming ability and larval duration. Recent studies on behavioral contributions to dispersal and recruitment during early life history stages have focused primarily on coral reef fishes. For cold ocean environments, strong seasonal variation in temperature and development times suggest that parallel studies of cold-water species on active swimming behavior that include measurements of swim speed and endurance are needed.

*Gadus morhua* (Atlantic cod) larvae and *Myoxocephalus scorpius* (shorthorn sculpin) larvae can swim immediately after hatch, and this ability increases rapidly in different trajectories. Critical swim speeds of both species have the potential to contribute significantly to dispersal through active vertical migration. The bottom-spawning sculpin hatched at a larger and more developed size than pelagic-spawning cod, and swimming ability improved at a faster rate for a given temperature; however, the ranges of swim speeds for comparably sized larvae were similar for both species during the pelagic phase. Given the similarity in swim speeds observed here for

different species for larvae of a given size, it appears that size may be a very useful general predictor of swim speeds during the early larval phase for other species of cold-water marine fishes. The temperature effect was especially important for sculpin in that it affected the development rate of critical swimming speed as a function of both age and size, whereas for cod larvae, temperature has a significant effect on the development rate of critical swimming speed only as a function of thermal summation age.

The two specific species in this study, which includes a pelagic and a bottom spawner in this study displayed very different sustained swimming ability immediately after hatch, and also improved quite differently. During the entire pelagic phase of cod, larval sustained swimming ability was absent or very weak, whereas sustained swimming ability of sculpin larvae improved steadily prior to settlement, and then improved rapidly after metamorphosis with accompanying habitat shift. If these patterns are also present in other bottom and pelagic spawners in Newfoundland waters, then larvae of bottom spawners may have greater potential to influence dispersal during early larval stages than in pelagic spawners. Temperature also plays a critical role in development and dispersal of early life history stages by affecting stage duration, development stage at hatch, development rate of sustained swimming ability, and muscle efficiency. Hatch temperature only leads to a faster swimming time increase rate as a function of absolute age for sculpin; however, lower temperature

surprisingly leads to a faster swimming time increase rate as a function of size for cod. At high temperatures, larvae display a stronger swimming ability at a given age and a shorter pelagic duration, whereas at lower temperatures larvae are relatively weaker swimmers that require a longer time to reach a given developmental stage or metamorphosis. Nonetheless, irrespective of temperature larvae attain a similar swimming ability at metamorphosis, albeit over different time periods. This convergence may help to offset temperature effects on dispersion.

Simple simulations of passive and active larval fish transport in Placentia Bay, Newfoundland suggest that active swimming performance, transport by currents, and environmental temperatures may all play significant roles in larval dispersal. However, the major dispersal component that differs between these bottom and pelagic spawners is the difference in swimming ability during the early pelagic phase. Field patterns support these predictions. The larval transport simulation and field observations suggests that the weak swimming ability of cod larvae contributes very little to dispersal compared to physical transport by the predominant current in the embayment, and that cod larvae may be considered as largely passive particles in the early pelagic dispersal. In contrast, sculpin larvae can exert active control of their dispersal from an early age. These simulation results suggest that if there is decreased survival outside of Placentia Bay (where there are expected to be more suitable nursery habitats), then larval retention within the bay should be advantageous. If this is true, then how do

relatively weak swimming larvae of pelagic spawners remain within the bay, or do they simply experience very high mortality?

Understanding fish larval dispersal requires that active swimming behaviour of larval fish and physical transport mechanisms both be taken into account. This study on cold-water species suggests that sculpin larvae from bottom spawners are strong swimmers that are able to make efficient use of motor skills for dispersal from an early age, whereas cod larvae from pelagic spawners are relatively weak swimmers that are largely passive and have little control on early pelagic larval transport. Sustained and critical swimming capabilities are only two aspects of larval biology that can enable fish larvae to influence dispersal. Several other important aspects of this question that remain to be addressed include changes in sustained and critical swimming abilities during ontogeny for other cold-water fishes, the extent of variation among species, and the degree to which these laboratory-based studies are realized in the field.





